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CORRELATION BETWEEN THE PERCENTAGE OF FAT IN COW'S MILK AND THE YIELD¹

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INTRODUCTION

It is a generally accepted opinion that cows with a large yield of milk produce a smaller percentage of fat than do cows with a small yield of milk. Stated in another way, it is thought that low-yielding cows produce a higher percentage of fat than that produced by high-yielding cows.

To what extent this is true or not true has not up to the present time been demonstrated by a careful statistical investigation. Wilson² from a study of the records of 2,866 Ayrshire cows concluded that quantity and quality (yield of milk and percentage of fat) were independent of each other. He states:

If we group together all the low-yielding cows, and find their milk invariably high in quality, we may infer that low yield and high quality are of the nature of concomitant variations. If we group the high-yielding cows together, and find their milk invariably of low quality, we may infer that high yield and low quality run together. But if we take these groups and any other groups we can form, and find that the quality varies the same way in them all—that is that there are low qualities, high qualities, and medium qualities in every one of them—then we are justified in inferring that the quantity and quality of the milk are independent of each other. And this is what we do find.

In a criticism of this work Pearson,³ by means of a correlation table, showed that there was a small but significant decrease in the percentage of fat with an increase in the yield of milk, and pointed out the fallacy of such a process of reasoning in connection with statistical data.

¹ Paper No. 3 from the Laboratory of Genetics, Agricultural Experiment Station of the University of Illinois.

² WILSON, James. THE SEPARATE INHERITANCE OF QUANTITY AND QUALITY IN COWS' MILK. *In* Sci. Proc. Roy. Dublin Soc., N. S., v. 12, no. 33, p. 470-475, 5 diagr. 1910.

³ PEARSON, Karl. NOTE ON THE SEPARATE INHERITANCE OF QUANTITY AND QUALITY IN COWS' MILK. *In* Biometrika, v. 7, No. 4, p. 548-550. 1910.

Wilson did not handle his data in such a way as to bring out the relationship which exists between the quantity and quality. In "The Principles of Stock-Breeding," Wilson¹ again writes:

In connection with yield and quality in milk, it has been assumed, frequently, that the two characters are interdependent: that when the one is high the other must be low. It has been found that this is not so. The characters are independent and have no effective influence upon each other. High quality of milk is found among cows giving all kinds of yield, and low quality is found similarly.

It seemed to the writer that it might be of some value to make a more careful statistical investigation of this question with our American cattle.

SOURCE OF DATA

In the registers of the different American associations is to be found a large body of data which furnished the major part of the material for this investigation. There are involved in this study the following: 2,141 yearly tests of Jerseys, Register of Merit, 1911, 1913; 3,564 Guernseys, Guernsey Breeders' Journal, May, 1915; 1,925 Holstein-Friesians, Holstein-Friesian Advanced Register Year Book, volumes 21-26; 1,091 Ayrshires, Year Book of the Ayrshire Breeders' Association, 1907, 1911, 1913, 1914; 98 Ayrshires²; 750 grade Jerseys³ and 341 grade Holstein-Friesians⁴; and 2,002⁴ yearly tests of cows unclassified as to breed.

Only the yearly tests were used for the reason that a yearly record is a more reliable criterion of a cow's performance and ability than a shorter test. It should be pointed out here, that in the case of the records from the associations, selected groups of individuals are involved in this study, since only selected individuals are subject to entry in the registers of the associations.

The method of finding the relation between the percentage of fat and the yield of milk is by means of the correlation table. The cows are grouped, according to age when the test began, into the following groups: 2 to 3 years, 3 to 4 years, 4 to 5 years, and 5 years and over. The last group comprises what are usually held to be mature cows. These are not exact divisions according to age, since a given group may contain individuals differing in age by almost a year. For example, the 3-to-4-year group contains those cows with tests beginning at some time after they were 3 and before they were 4 years old. A cow with a test beginning the day she was 3 would be practically a year younger than one having a test starting when she was one day under 4, though both would be classed in the same group. Of course, there are few cases of this kind.

¹ WILSON, JAMES. THE PRINCIPLES OF STOCK-BREEDING. P. 121-122. London, 1912.

² Furnished by Mr. C. M. Winslow, Secretary of the Ayrshire Breeders' Association.

³ Obtained from Mr. W. W. Yapp, Illinois Agricultural Experiment Station.

⁴ Obtained from Prof. W. J. Fraser, Illinois Agricultural Experiment Station.

POSSIBLE SOURCES OF ERROR

In some of the breeds, Jersey and Guernsey, a yearly test consists of any 365 consecutive days. This may cover parts of two lactation periods, which is not a serious objection, since the study is interested in the relation between the percentage of butter fat and yield of milk in groups of individuals and not in the individual herself. In other words, the question is to what extent, if any, do cows with large milk yield tend to show a low percentage of fat, or cows with a low milk yield to show a high percentage. The Ayrshire Association specifies both the amount of milk and butter fat necessary for entrance. In the other associations only the butter-fat yield is specified. Unless the requirements of the Ayrshire Association are in accordance with the natural relation of butter-fat and milk yield, one would expect to find abnormal results in such a selected group, which would not hold for Ayrshire cattle in general. This point will be treated more fully later in this paper. For the grade Jerseys, grade Holstein-Friesians, and cows unclassified as to breed, it should be pointed out that the populations are composed of a heterogeneous lot, and whatever results are found will apply only to such mixed populations.

ANALYSIS OF DATA

JERSEY

Tables I to IV show, in the form of correlation tables, the distribution of individuals with regard to the yield of milk and the percentage of fat. Table V contains all the tests of Jerseys regardless of age and was made by combining Tables I to IV. Text Table A summarizes the means, standard deviations, coefficients of variability of milk and fat, and the correlation between the percentage of fat and the yield for Jerseys of different ages, and for Jerseys, irrespective of age.

TABLE A.—Summary of results from a study of the correlation between the percentage of fat and yield of milk for Jerseys

[Fat in percentage; milk in pounds]

Age.	Number of animals.	Type of test.	Mean.	Standard deviation.	Coefficient of variability.	Correlation.
<i>Years.</i>						
2 to 3.....	877	Milk.....	6,475.0 ± 28.9	1,270.5 ± 20.5	19.62 ± 0.31	-0.360 ± 0.020
		Fat.....	5.425 ± 0.012	0.517 ± 0.008	9.42 ± 0.15	
3 to 4.....	411	Milk.....	7,375.0 ± 45.8	1,377.5 ± 32.4	18.81 ± 0.15	-0.437 ± 0.007
		Fat.....	5.401 ± 0.019	0.562 ± 0.013	10.41 ± 0.25	
4 to 5.....	219	Milk.....	8,043.4 ± 60.7	1,332.5 ± 42.9	16.57 ± 0.55	-0.359 ± 0.040
		Fat.....	5.463 ± 0.024	0.533 ± 0.017	9.76 ± 0.32	
5 and over.....	634	Milk.....	8,814.5 ± 43.3	1,608.3 ± 36.3	18.45 ± 0.33	-0.397 ± 0.023
		Fat.....	5.322 ± 0.013	0.502 ± 0.010	9.44 ± 0.18	
All ages.....	2,247	Milk.....	7,491.4 ± 25.0	1,178.0 ± 17.7	22.93 ± 0.25	-0.354 ± 0.013
		Fat.....	5.392 ± 0.008	0.525 ± 0.005	9.74 ± 0.10	

The correlation is negative and very significant for all ages. When judged by their probable errors, there are no significant differences among the correlations for the different groups.

The milk yield increases from an average of 6,475 pounds for the 2-to-3-year-old class to 8,814.5 pounds for the mature class (fig. 1). Since

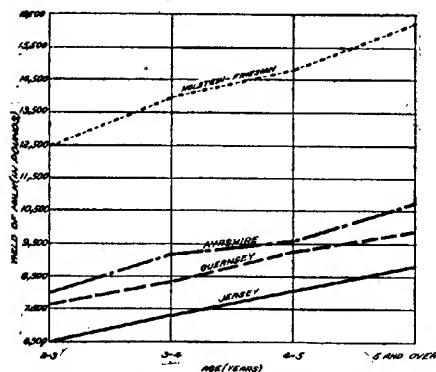


FIG. 1.—Graphs showing the averages of the milk yield for the different ages of cows.

3-to-4-year-old class, though the difference is not significant (fig. 2). On the whole, the percentage remains practically the same. This may be due to the relatively stable relation between the amount of fat and yield throughout the growing period of the individual cow. Holdaway¹ found this to be true for Holstein-Friesians, using the 7-day records.

Stated in another way, the percentage of fat seems to be fairly constant throughout the life of a given individual, but different individuals show differing percentages of fat. The results show that at a given age cows with a high milk yield tend to produce a lower percentage of

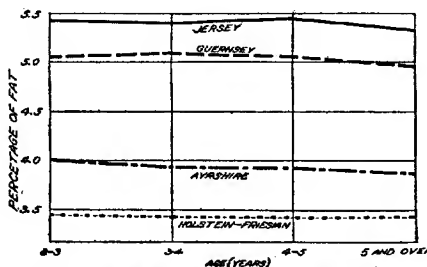


FIG. 2.—Graphs showing the averages of percentages of butter fat for different breeds of cows.

fat than do cows with a low milk yield. This is expressed by the negative correlations obtained. Table B illustrates in another way that this is true. This table is the result of arbitrarily dividing Table II into three parts, cows yielding 4,500 to 6,500, those yielding 7,000 to 9,000,

¹ HOLDAWAY, C. W. STATISTICAL WEIGHTING FOR AGE OF ADVANCED REGISTRY COWS. *IN* AMER. NAT., v. 50, no. 599, p. 676-687, 3 fig. 1916.

and those yielding 9,500 to 13,000 pounds of milk, and finding the average yield of milk and percentage of fat. The decrease from 5.657 per cent for the first group to 4.941 per cent for the third group is very significant. Any group of cows showing a negative correlation between percentage of fat and yield of milk would give, in general, the same results if treated as was Table II.

TABLE B.—Milk yield and percentage of butter fat of Jerseys 3 to 4 years of age

Number of animals.	Extremes of milk yield.	Average milk yield.	Average percentage of fat.
	Pounds.	Pounds.	
152.....	4,500-6,500	6,049.3	5.657
220.....	7,000-9,000	7,677.3	5.307
39.....	9,500-13,000	10,307.7	4.941

GUERNSEY

Tables VI to IX show the distribution of individuals with regard to the yield of milk and the percentage of butter fat, in the form of correlation tables. Table X combines Tables VI to IX. Table C gives the means, standard deviations, coefficients of variability of milk and fat, and the correlation between the percentage of fat and yield of milk for Guernseys of different ages.

TABLE C.—Summary of results from a study of the correlation between the percentage of fat and yield of milk for Guernseys

[Fat in percentage; milk in pounds]

Age.	Number of animals.	Type of test.	Mean.	Standard deviation.	Coefficient of variability.	Correlation.
Years.						
2 to 3.....	1,375	Milk.....	7,608.0 ± 28.8	1,584.0 ± 20.4	20.82 ± 0.77	-0.251 ± 0.017
		Fat.....	5.065 ± 0.008	0.458 ± 0.006	9.03 ± 0.12	
3 to 4.....	644	Milk.....	8,317.0 ± 49.3	1,854.0 ± 34.8	22.29 ± 0.44	-0.269 ± 0.024
		Fat.....	5.080 ± 0.013	0.477 ± 0.009	9.39 ± 0.18	
4 to 5.....	478	Milk.....	9,247.0 ± 62.6	2,030.0 ± 44.3	21.95 ± 0.50	-0.264 ± 0.020
		Fat.....	5.046 ± 0.014	0.466 ± 0.010	9.13 ± 0.20	
5 and over.....	1,067	Milk.....	9,893.0 ± 42.8	2,067.5 ± 30.2	20.90 ± 0.68	-0.337 ± 0.018
		Fat.....	4.956 ± 0.010	0.478 ± 0.007	9.64 ± 0.30	
All ages.....	3,564	Milk.....	8,644.4 ± 21.7	2,095.4 ± 16.7	24.24 ± 0.10	-0.296 ± 0.010
		Fat.....	5.033 ± 0.005	0.471 ± 0.004	9.35 ± 0.08	

The correlation coefficients are negative as in the case of the Jerseys, but slightly smaller. For the Jerseys they range from -0.359 ± 0.040 to -0.437 ± 0.027 , while for the Guernseys the range is from -0.251 ± 0.017 to -0.337 ± 0.018 . The yield of milk gradually increases from an average of 7,608 pounds for the 2-to-3-year-old class to 9,893 for the group which is 5 years and over. The average percentage of fat varies from 4.956 ± 0.010 for the group which is 5 years and over to 5.080 ± 0.013 for the 3-to-4-year-old class. (See fig. 2.)

HOLSTEIN-FRIESIAN

Tables XI to XIV exhibit the distributions of individuals with regard to the yield of milk and the percentage of fat in the form of correlation tables. Table XV combines Tables XI to XIV. Table D summarizes the means, standard deviations, coefficients of variability for milk and fat, and the correlations between percentage of fat and yield for Holstein-Friesians of different ages.

TABLE D.—Summary of results from a study of the correlation between the percentage of fat and yield of milk for Holstein-Friesians

[Fat in percentage; milk in pounds]

Age.	Number of animals.	Type of test.	Mean	Standard deviation.	Coefficient of variability.	Correlation.
<i>Years.</i>						
2 to 3.....	670	Milk.....	12,488.5 ± 80.4	2,942.0 ± 56.8	23.56 ± 0.48	-0.116 ± 0.027
		Fat.....	3.462 ± 0.008	0.294 ± 0.006	8.50 ± 0.16	
3 to 4.....	341	Milk.....	13,938.5 ± 116.5	3,188.0 ± 82.4	22.87 ± 0.62	-0.160 ± 0.039
		Fat.....	3.433 ± 0.012	0.322 ± 0.008	9.38 ± 0.24	
4 to 5.....	292	Milk.....	14,825.5 ± 124.4	3,151.0 ± 87.9	21.25 ± 0.62	-0.088 ± 0.039
		Fat.....	3.417 ± 0.012	0.313 ± 0.009	9.17 ± 0.28	
5 and over.....	682	Milk.....	16,280.0 ± 94.4	3,654.5 ± 66.7	22.45 ± 0.43	-0.115 ± 0.026
		Fat.....	3.420 ± 0.008	0.301 ± 0.006	8.81 ± 0.16	
All ages.....	1,925	Milk.....	14,443.1 ± 56.0	3,640.7 ± 39.6	25.21 ± 0.29	-0.133 ± 0.015
		Fat.....	3.435 ± 0.005	0.305 ± 0.003	8.88 ± 0.10	

The correlations are much smaller for the Holstein-Friesian than for the two preceding breeds. They range from -0.088 ± 0.039 to -0.160 ± 0.036 . The first is not significant when judged by the probable error. The milk yields increase regularly from 12,488 pounds for the youngest class to 16,280 for the oldest. The percentages of fat remain practically constant for the different ages. (See fig. 2.)

AYRSHIRE

Tables XVI to XIX are correlation tables for the different classes of Ayrshires. Table E gives means, standard deviations, coefficients of variability for milk and fat, and the correlations between percentages of fat and yield of milk.

TABLE E.—Summary of results from a study of the correlation between the percentage of fat and yield of milk for Ayrshires

[Fat in percentage; milk in pounds]

Age.	Number of animals.	Type of test.	Mean	Standard deviation.	Coefficient of variability.	Correlation.
<i>Years.</i>						
2 to 3.....	343	Milk.....	7,960.5 ± 47.9	1,314.5 ± 33.9	16.51 ± 0.44	+0.019 ± 0.036
		Fat.....	4.016 ± 0.011	0.310 ± 0.008	7.71 ± 0.20	
3 to 4.....	192	Milk.....	9,179.5 ± 86.1	1,769.5 ± 60.9	19.28 ± 0.69	-0.093 ± 0.048
		Fat.....	3.936 ± 0.014	0.314 ± 0.011	6.35 ± 0.28	
4 to 5.....	160	Milk.....	9,580.5 ± 83.5	1,566.5 ± 59.1	16.34 ± 0.63	-0.023 ± 0.053
		Fat.....	3.919 ± 0.016	0.303 ± 0.011	7.73 ± 0.29	
5 and over.....	396	Milk.....	10,726.0 ± 67.1	1,980.0 ± 47.5	18.46 ± 0.46	-0.047 ± 0.034
		Fat.....	3.805 ± 0.011	0.313 ± 0.008	8.10 ± 0.19	
All ages.....	1,091	Milk.....	9,417.1 ± 41.7	2,044.4 ± 29.3	21.71 ± 0.33	-0.138 ± 0.020
		Fat.....	3.933 ± 0.006	0.318 ± 0.005	8.08 ± 0.12	

In no one of the four groups classified as to age is there a significant correlation, meaning that for these classes of individuals studied the milk yield and percentage of fat are independent. It is curious that this breed should have a different relation existing between fat and milk than that of the Jerseys, Guernseys, and Holstein-Friesians. This result is probably due to the fact that they are a much more highly selected group of individuals than in the case of any of the other breeds, owing to the requirements for registry imposed by the Ayrshire Association. The minimum requirements are as follows:

Age.	Weight of milk.	Weight of fat.
Years.	Pounds.	Pounds.
2 to 3.....	6,000	214.3
3 to 4.....	6,500	236.0
4 to 5.....	7,500	279.0
5 and over.....	8,500	322.0

This would mean that upon the basis of these specified amounts the percentages of fat for the different ages would be as follows:

2 to 3 years.....	3.572
3 to 4 years.....	3.631
4 to 5 years.....	3.720
5 years and over.....	3.788

A gradual increase in the percentage of fat as the age increases is to be noted. This is contrary to what was found to exist for the other breeds. For Table XX, constructed from Tables XVI to XIX, a correlation of -0.138 ± 0.020 is found. This is practically the same correlation found for the Holstein-Friesian cows. This negative correlation resulting from combining the subgroups of Ayrshires is to be expected, since there is an increase in the milk yield with age and a decrease in the percentage of fat. (See Table E.) It may be that the requirements for entry in the register of the Ayrshire Association tend to eliminate high-yielding cows with a low percentage of fat and low-yielding cows with a high percentage of fat.

The correlation between the yield and percentage of fat for 98 Ayrshire cows which were tested and failed to meet the requirements was found to be

$$r = -0.226 \pm 0.065.$$

A larger number of such tests would be necessary to determine whether a difference exists between cows which meet the requirements and those which do not.

The percentage of butter fat among these 98 tests decreases with age as in Table E, as follows:

Number of animals.	Age.	Percentage of fat.
	<i>Years.</i>	
19	2 to 3.....	4.112
22	3 to 4.....	4.035
20	4 to 5.....	3.997
37	5 and over...	3.842

The work of Speir¹ shows that there is a slight tendency for the percentage of fat to decrease in Ayrshires after the third year. Both Jerseys and Guernseys of 5 years of age and over show a slight decrease. (See Tables A and B.) The mature class of Holstein-Friesian cows, however, does not show a decrease (Table C).

COWS NOT PURE-BRED

The writer thought it would be of interest to see the extent of correlation between the yield and percentage of fat in cows not pure-bred. Grade Jerseys, grade Holsteins-Friesians, and cows unclassified as to breed are considered.

Tables F, G, and H give the results of the study for the different classes in the order given above.

TABLE F.—Summary of results from a study of the correlation between the percentage of fat and yield of milk for grade Jerseys

[Fat in percentage; milk in pounds]

Age.	Number of animals.	Type of test.	Mean.	Standard deviation.	Coefficient of variability.	Correlation.
<i>Years.</i>						
2 to 3.....	101...	Milk.....	4,663.5 ± 81.7	1,217.0 ± 57.8	26.10 ± 1.32	} -0.114 ± 0.066
		Fat.....	5,106 ± 0.033	0.469 ± 0.023	9.57 ± 0.45	
3 to 4.....	155...	Milk.....	5,035.5 ± 71.5	1,316.0 ± 50.4	26.13 ± 1.07	} -0.214 ± 0.051
		Fat.....	5,124 ± 0.023	0.592 ± 0.023	11.56 ± 0.45	
4 to 5.....	146...	Milk.....	5,208.0 ± 71.5	1,281.5 ± 50.6	24.19 ± 1.01	} -0.272 ± 0.052
		Fat.....	5,068 ± 0.029	0.520 ± 0.021	10.26 ± 0.41	
5 and over.....	348...	Milk.....	5,504.5 ± 48.1	1,329.0 ± 34.0	24.14 ± 0.65	} -0.138 ± 0.035
		Fat.....	4,923 ± 0.022	0.606 ± 0.016	12.32 ± 0.32	

¹ SPEIR, John. MILK RECORDS. In Trans. Highland and Agr. Soc. Scotland, s. 5, v. 16, p. 170-229, fig. 18-20. 1904.

TABLE G.—Summary of results from a study of the correlation between the percentage of fat and yield of milk for grade Holstein-Friesians¹

[Fat in percentage; milk in pounds]

Age.	Number of animals.	Type of test.	Mean.	Standard deviation.	Coefficient of variability.	Correlation.
<i>Years.</i>						
2 to 3.....	76.....	Milk.....	5,776.5 ± 113.4	1,465.5 ± 80.2	25.37 ± 1.48	-0.311 ± 0.074
		Fat.....	3.688 ± 0.028	0.161 ± 0.020	9.80 ± 0.54	
3 to 4.....	88.....	Milk.....	6,727.5 ± 112.1	1,559.0 ± 79.1	23.17 ± 1.24	-0.345 ± 0.063
		Fat.....	3.508 ± 0.025	0.144 ± 0.018	9.04 ± 0.49	
4 to 5.....	41.....	Milk.....	7,305.0 ± 114.8	2,039.5 ± 131.9	27.92 ± 1.73	-0.155 ± 0.103
		Fat.....	3.581 ± 0.041	0.391 ± 0.029	10.92 ± 0.83	
5 and over.....	136.....	Milk.....	7,441.0 ± 104.1	1,799.0 ± 73.6	24.18 ± 1.05	-0.212 ± 0.058
		Fat.....	3.546 ± 0.025	0.440 ± 0.018	13.39 ± 0.51	

TABLE H.—Summary of results from a study of the correlation between the percentage of fat and yield of milk for cows unclassified as to breed

[Fat in percentage; milk in pounds]

Age.	Number of animals.	Type of test.	Mean.	Standard deviation.	Coefficient of variability.	Correlation.
All ages.....	2,002.....	Milk.....	5,824.6 ± 28.5	1,838.2 ± 20.1	32.47 ± 0.38	-0.359 ± 0.013
		Fat.....	3.902 ± 0.009	0.175 ± 0.006	14.75 ± 0.16	

There is a very significant negative correlation between the yield and percentage of fat for all three classes of cows represented by the three foregoing tables (Tables F-H).

CONCLUSIONS

(1) A significant negative correlation exists between the percentage of fat in cows' milk and the yield for the Jerseys, Guernseys, Holstein-Friesians, grade Jerseys, grade Holstein-Friesians, and cows unclassified as to breed. The correlation for Ayrshires is not significant in the subgroups classed in respect to age, but it is significant when these groups are treated as a whole. (See Tables XXI and F, G, H.)

(2) The yield of milk increases with age. However, since all cows 5 years of age and over are classed together, it may well be that the yield decreases at some period beyond 5 years. Pearl and Patterson¹ showed that in Jersey cows using the 7-day records that the maximum production is reached between the eighth and ninth year. Crowther² from records of Ayrshires is of the opinion that maximum production is close to the eighth year. (See Table XXI and fig. 1.)

(3) In the Jerseys, Guernseys, and Holstein-Friesians the percentage of fat remains fairly constant for the different ages studied. However,

¹ PEARL, Raymond, and PATTERSON, S. W. THE CHANGE OF MILK FLOW WITH AGE, AS DETERMINED FROM THE SEVEN-DAY RECORDS OF JERSEY COWS. *Maine Agr. Exp. Sta. Bul.* 262, p. 145-153, fig. 1. 1917.

² CROWTHER, Charles. VARIATION IN THE COMPOSITION OF COW'S MILK. *1st Jour. Agr. Sci.*, v. 1, pt. 2, p. 149-175. 1905.

the group 5 years of age and over in the Jerseys and Guernseys shows a slightly lower percentage of fat than the younger groups. In the case of the Ayrshires, there is a gradual decrease with age. Between the youngest and oldest groups there is a difference of 0.151 per cent. (See Table XXI and fig. 2.)

(4) When judged by the standard deviation, age has no influence on the variability of the percentage of butter fat. But the class 5 years of age and over is more variable in the yield of milk than the younger groups. This may occur because of the inclusion in this group of old cows whose milk yield has decreased. (See Table XXI.)

(5) The breed has an influence on the variability of milk yield and percentage of fat, using the standard deviation as a basis of comparison. For variability in yield the breeds stand in the following order in an ascending scale: Jersey, Ayrshire, and Guernsey practically the same, Holstein-Friesian. For percentage of fat, the order is: Holstein-Friesian and Ayrshire about the same, Guernsey, Jersey. (See Table XXI.)

(6) For the production of milk the breeds stand as follows (see Table XXI.)

	Pounds.
Holstein-Friesian.....	14,443.1
Ayrshire.....	9,417.1
Guernsey.....	8,644.4
Jersey.....	7,491.4

(7) The average percentages of fat for the different breeds are as follows (see Table XXI.)

	Pounds.
Jersey.....	5.392
Guernsey.....	5.033
Ayrshire.....	3.933
Holstein-Friesian.....	3.435

TABLE I.—Correlation between the percentage of fat in cow's milk and the yield—Registered Jerseys 2 to 3 years of age

Yield of milk, in pounds.	Percentage of fat																				Total									
	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0	6.1		6.2	6.3	6.4	6.5	6.6	6.7	6.8	6.9	7.0
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Total	2	4	16	19	30	41	33	47	59	67	68	61	47	45	39	48	31	22	14	16	7	8	2	4	0	2	4	0	2	877

Yield of milk, in pounds.

r = 0.100 to 0.200

$r = -0.36 \pm 0.008$

TABLE II.—Correlation between the percentage of fat in cow's milk and the yield—Registered Jerseys 3 to 4 years of age

Yield of milk, in pounds	Percentage of fat																				Total																
	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9		6.0	6.1	6.2	6.3	6.4	6.5	6.6	6.7	6.8	6.9	7.0	7.1	7.2	7.3	Total	
4,500.....																																					11
5,000.....																																					20
5,500.....																																					47
6,000.....																																					69
6,500.....																																					71
7,000.....																																					67
7,500.....																																					35
8,000.....																																					28
8,500.....																																					15
9,000.....																																					8
9,500.....																																					4
10,000.....																																					50
10,500.....																																					1
11,000.....																																					1
11,500.....																																					1
12,000.....																																					1
12,500.....																																					1
13,000.....																																					1
Total.....	1	1	3	4	5	9	14	12	17	21	24	22	34	33	24	32	35	21	22	22	18	10	5	6	7	1	1	6	0	0	0	0	1	411			

r = -0.437 ± 0.027

TABLE III.—Correlation between the percentage of fat in cow's milk and the yield—Registered Jerseys 4 to 5 years of age

Yield of milk, in pounds	Percentage of fat																				Total					
	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0	6.1	6.2	6.3		6.4	6.5	6.6	6.7	6.8
5,500																										1
6,000																										1
6,500																										1
7,000																										1
7,500																										1
8,000																										1
8,500																										1
9,000																										1
9,500																										1
10,000																										1
10,500																										1
11,000																										1
11,500																										1
12,000																										1
12,500																										1
13,000																										1
13,500																										1
14,000																										1
Total.....	3	5	6	3	8	12	21	9	16	16	13	16	14	12	22	21	9	3	13	4	5	1	5	1	3	219

 $r = -0.339 \pm 0.040$

Yield of milk, in pounds

TABLE IV.—Correlation between the percentage of fat in cow's milk and the yield—Registered Jerseys 5 years and over

Yield of milk in pounds	Percentage of fat																									Total.				
	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0	6.1	6.2	6.3	6.4		6.5	6.6	6.7	6.8
5,500																														3
6,000																														10
6,500																														66
7,000																														66
7,500																														103
8,000																														76
8,500																														76
9,000																														60
9,500																														43
10,000																														37
10,500																														37
11,000																														10
11,500																														10
12,000																														9
12,500																														8
13,000																														5
13,500																														5
14,000																														2
14,500																														2
15,000																														1
15,500																														1
16,000																														0
16,500																														0
Total	1	1	4	7	9	16	19	22	29	39	48	49	41	50	59	46	38	26	31	23	26	15	12	5	5	4	4	2	2	634

$$r = -0.397 \pm 0.003$$

TABLE V.—Correlation between the percentage of fat in cow's milk and the yield—Registered Jerseys, all ages

Yield of milk, in pounds	Percentage of fat																				Total										
	4.0-4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5	6.6	6.7	6.8	6.9	7.0	7.1	7.2	7.3	Total
4,000.....																															10
4,500.....																															10
5,000.....																															10
5,500.....																															10
6,000.....																															10
6,500.....																															10
7,000.....																															10
7,500.....																															10
8,000.....																															10
8,500.....																															10
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15,000.....																															10
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34,500.....																															10
35,000.....																															10
35,500.....																															10
36,000.....																															10
36,500.....																															10
37,000.....																															10
37,500.....																															10
38,000.....																															10
38,500.....																															10
39,000.....																															10
39,500.....																															10
40,000.....																															10
Total.....	3	3	9	15	33	43	59	63	95	110	140	169	191	191	191	191	191	191	191	191	191	191	191	191	191	191	191	191	191	191	191

$r = -0.34 \pm 0.01$

Yield of milk, in pounds

TABLE VI.—Correlation between the percentage of fat in cow's milk and the yield—Registered Guernseys 2 to 3 years of age

Percentage of fat

	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5	6.6	6.7	Total
4,500.....																																3
5,000.....																																14
5,500.....																																167
6,000.....																																169
6,500.....																																159
7,000.....																																157
7,500.....																																154
8,000.....																																148
8,500.....																																152
9,000.....																																152
9,500.....																																158
10,000.....																																168
10,500.....																																46
11,000.....																																40
11,500.....																																19
12,000.....																																18
12,500.....																																4
13,000.....																																6
13,500.....																																1
14,000.....																																1
14,500.....																																1
15,000.....																																0
Total.....	1	1	0	3	16	24	38	38	38	38	96	102	107	110	114	113	96	99	85	56	38	29	20	14	7	11	3	2	3	9	1	5,375

Yield of milk, in pounds

r = -0.31±0.017

TABLE VII.—Correlation between the percentage of fat in cow's milk and the yield—Registered Guernseys 3 to 4 years of age

Yield of milk, in pounds	Percentage of fat																				Total
	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	
5,000																					1
6,000																					1
7,000																					1
8,000																					1
9,000																					1
10,000																					1
11,000																					1
12,000																					1
13,000																					1
14,000																					1
15,000																					1
16,000																					1
17,000																					1
18,000																					1
19,000																					1
20,000																					1
21,000																					1
22,000																					1
23,000																					1
24,000																					1
25,000																					1
26,000																					1
27,000																					1
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31,000																					1
32,000																					1
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34,000																					1
35,000																					1
36,000																					1
37,000																					1
38,000																					1
39,000																					1
40,000																					1
41,000																					1
42,000																					1
43,000																					1
44,000																					1
45,000																					1
46,000																					1
47,000																					1
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68,000																					1
69,000																					1
70,000																					1
71,000																					1
72,000																					1
73,000																					1
74,000																					1
75,000																					1
76,000																					1
77,000																					1
78,000																					1
79,000																					1
80,000																					1
81,000																					1
82,000																					1
83,000																					1
84,000																					1
85,000																					1
86,000																					1
87,000																					1
88,000																					1
89,000																					1
90,000																					1
91,000																					1
92,000																					1
93,000																					1
94,000																					1
95,000																					1
96,000																					1
97,000																					1
98,000																					1
99,000																					1
100,000																					1
Total	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	644

 $r = -0.385 \pm 0.004$

TABLE VIII.—Correlation between the percentage of fat in cow's milk and the yield—Registered Guernseys 4 to 5 years of age

Yield of milk, in pounds	Percentage of fat																												Total.				
	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5		6.6	6.7	6.8	6.9
5,500.....																																	2
6,000.....																																	6
6,500.....																																	19
7,000.....																																	41
7,500.....																																	47
8,000.....																																	70
8,500.....																																	59
9,000.....																																	43
9,500.....																																	38
10,000.....																																	26
10,500.....																																	33
11,000.....																																	15
11,500.....																																	4
12,000.....																																	10
12,500.....																																	1
13,000.....																																	1
13,500.....																																	1
14,000.....																																	1
14,500.....																																	1
15,000.....																																	1
15,500.....																																	1
16,000.....																																	1
16,500.....																																	1
17,000.....																																	1
17,500.....																																	1
Total.....	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	478	

r = -0.561 ± 0.059

Yield of milk, in pounds

TABLE IX.—Correlation between the percentage of fat in cow's milk and the yield—Registered Guernseys 5 years and over

Yield of milk, in pounds	Percentage of fat																				Total.									
	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6		5.7	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5
6,000.																														1
6,500.																														15
7,000.																														73
7,500.																														101
8,000.																														130
8,500.																														103
9,000.																														93
9,500.																														84
10,000.																														46
10,500.																														44
11,000.																														30
11,500.																														19
12,000.																														14
12,500.																														6
13,000.																														1
13,500.																														1
14,000.																														1
14,500.																														1
15,000.																														1
15,500.																														1
16,000.																														1
16,500.																														1
17,000.																														1
17,500.																														1
18,000.																														1
18,500.																														1
19,000.																														1
19,500.																														1
Total	3	1	6	8	10	25	41	53	71	71	74	100	75	84	94	70	60	50	40	33	26	24	15	9	7	6	2	2	1,067	

r = -0.337 ± 0.018.

TABLE X.—Correlation between the percentage of fat in cow's milk and the yield—Registered Guernseys, all ages

Yield of milk, in pounds	Percentage of fat																				Total.													
	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6		5.7	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5	6.6	6.7	6.8	6.9
4,500.....																																		36
5,000.....																																		103
5,500.....																																		210
6,000.....																																		210
6,500.....																																		238
7,000.....																																		373
7,500.....																																		370
8,000.....																																		319
8,500.....																																		319
9,000.....																																		279
9,500.....																																		188
10,000.....																																		176
10,500.....																																		176
11,000.....																																		61
11,500.....																																		52
12,000.....																																		31
12,500.....																																		15
13,000.....																																		15
13,500.....																																		20
14,000.....																																		10
14,500.....																																		4
15,000.....																																		1
15,500.....																																		1
16,000.....																																		1
16,500.....																																		1
17,000.....																																		1
17,500.....																																		1
18,000.....																																		1
18,500.....																																		1
19,000.....																																		1
19,500.....																																		1
Total.....	4	4	8	16	41	68	111	122	187	311	246	275	275	294	305	273	241	216	204	135	87	76	52	42	21	20	10	7	3	1	1	1	3,564	

$r = -0.396 \pm 0.010$

Yield of milk, in pounds

TABLE XI.—Correlation between the percentage of fat in cow's milk and the yield—Registered Holstein-Friesians 2 to 3 years of age

Yield of milk, in pounds	Percentage of fat																				Total.
	2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4		
6,000																				1	
6,500																				1	
7,000																				4	
7,500																				12	
8,000																				13	
8,500																				25	
9,000																				33	
9,500																				26	
10,000																				38	
10,500																				28	
11,000																				32	
11,500																				53	
12,000																				37	
12,500																				34	
13,000																				41	
13,500																				30	
14,000																				29	
14,500																				24	
15,000																				26	
15,500																				50	
16,000																				19	
16,500																				18	
17,000																				9	
17,500																				8	
18,000																				10	
18,500																				4	
19,000																				5	
19,500																				3	
20,000																				2	
20,500																				1	
21,000																				3	
21,500																				0	
22,000																				1	
22,500																				0	
23,000																				1	
Total.	1	2	3	14	24	42	61	68	85	77	81	62	30	25	9	10	7	2	1	610	

$$r = -0.116 \pm 0.027.$$

BLE XII.—*Correlation between the percentage of fat in cow's milk and the yield—Registered Holstein-Friesians 3 to 4 years of age*

Percentage of fat

	2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	Total
8,000.....												1	1								2
8,500.....											1	1	1								3
9,000.....							1	1	1	2	2	1	4								12
9,500.....								2	1	1	2	1			1	2					12
10,000.....									2	3	4	1	1								12
10,500.....							1	2		2	6	2	3								16
11,000.....								1	4	3		1	1	3	2						16
11,500.....			1				1	2	2	4	1	1	1	2	1						18
12,000.....			1	1	1	2	1	2	4	2		2	1	1							18
12,500.....						1		1	4	4	1	2									18
13,000.....			1	1	1	2	1	1	5	2	1	2	1		1			1	1		20
13,500.....			2	1	4	5	3	3	3	7	2	3	1	1	1						36
14,000.....	1	1	1		2	3	2	2	2		1	2									18
14,500.....	1	1			2		2	5	2	4	2	1	1	2							22
15,000.....					3		2	3	2	2	2			1	2	2					14
15,500.....				2	1		1	1	3		3										15
16,000.....			1	2	2	3		3	2	1											15
16,500.....					2		5	1		2	2										12
17,000.....					2	1				2			1								6
17,500.....					1	2		1	5		1		1		1						15
18,000.....								1	1	1											5
18,500.....				1	1		2	1	2												8
19,000.....				1				1	2	2	1										8
19,500.....								1	1	2											4
20,000.....			1	1	1			2													4
20,500.....																					1
21,000.....											1										2
21,500.....						1				1											2
22,000.....																					0
22,500.....									1						1						3
23,000.....																					2
23,500.....																					0
24,000.....					1																1
24,500.....																					1
Total ...	2	2	6	11	16	27	30	42	52	34	42	20	27	12	7	4	2	2	1	2	341

$$r = -0.166 \pm 0.036$$

TABLE XIII.—Correlation between the percentage of fat in cow's milk and the yield—Registered Holstein-Friesians 4 to 5 years of age

	Percentage of fat																	Total
	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	
8,000.....																		1
8,500.....																		1
9,000.....																		2
9,500.....																		3
10,000.....																		3
10,500.....																		9
11,000.....																		14
11,500.....																		14
12,000.....																		19
12,500.....																		17
13,000.....																		13
13,500.....																		21
14,000.....																		20
15,000.....																		10
15,500.....																		10
16,000.....																		15
16,500.....																		10
17,000.....																		11
17,500.....																		12
18,000.....																		4
18,500.....																		10
19,000.....																		5
19,500.....																		5
20,000.....																		5
20,500.....																		5
21,000.....																		2
21,500.....																		2
22,000.....																		2
22,500.....																		0
23,000.....																		0
23,500.....																		0
24,000.....																		4
Totals.....	2	2	1	11	19	19	37	31	32	39	30	20	12	13	10	3	0	293

$$r = -0.88 \pm 0.039$$

TABLE XIV.—Correlation between the percentage of fat in cow's milk and the yield—
Registered Holstein-Friesians 5 years and over

[illegible]

$$r = -0.115 \pm 0.026$$

TABLE XV.—Correlation between the percentage of fat in cow's milk and the yield—
Registered Holstein-Friesians, all ages

Yield of milk, in pounds	Percentage of fat																								Total.	
	2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9		
6,000																										1
6,500																										1
7,000																										1
7,500																										1
8,000																										16
8,500																										39
9,000																										40
9,500																										33
10,000																										55
10,500																										38
11,000																										38
11,500																										106
12,000																										111
12,500																										115
13,000																										113
13,500																										108
14,000																										115
14,500																										99
15,000																										86
15,500																										91
16,000																										75
16,500																										80
17,000																										73
17,500																										72
18,000																										51
18,500																										30
19,000																										35
19,500																										27
20,000																										34
20,500																										25
21,000																										12
21,500																										12
22,000																										16
22,500																										13
23,000																										8
23,500																										0
24,000																										0
24,500																										0
25,000																										0
25,500																										0
26,000																										0
26,500																										0
27,000																										0
27,500																										0
28,000																										0
28,500																										

$$r = -0.133 \pm 0.015$$

TABLE XVI.—Correlation between the percentage of fat in cow's milk and the yield—Registered Ayrshires 2 to 3 years of age

Yield of milk, in pounds	Percentage of fat																										Total
	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	
5,000.....								1																			1
6,000.....							1																				1
7,000.....							1																				1
8,000.....							1																				1
9,000.....							1																				1
10,000.....							1																				1
11,000.....							1																				1
12,000.....							1																				1
13,000.....							1																				1
Total.....	1	1	1	1	1	1	1	34	40	50	44	31	25	11	3	4	3	0	0	0	0	0	0	0	0	1	343

r = +0.019 ± 0.036.

TABLE XVII.—Correlation between the percentage of fat in cow's milk and the yield—Registered Ayrshires 3 to 4 years of age

Yield of milk, in pounds	Percentage of fat																	Total
	3.0	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	
6,500																		5
7,000																		10
7,500																		24
8,000																		23
8,500																		35
9,000																		20
9,500																		17
10,000																		10
10,500																		11
11,000																		7
11,500																		3
12,000																		3
12,500																		3
13,000																		3
13,500																		3
14,000																		1
14,500																		3
15,000																		2
Total	1	0	0	4	10	7	14	18	20	21	23	19	17	16	6	7	1	192

$$r = -0.093 \pm 0.048$$

TABLE XVIII.—Correlation between the percentage of fat in cow's milk and the yield—Registered Ayrshires 4 to 5 years of age

Yield of milk, in pounds	Percentage of fat																	Total
	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	
7,500																		3
8,000																		27
8,500																		21
9,000																		29
9,500																		27
10,000																		19
10,500																		16
11,000																		6
11,500																		5
12,000																		3
12,500																		3
13,000																		2
13,500																		2
14,000																		0
14,500																		0
15,000																		0
15,500																		0
16,000																		0
16,500																		0
17,000																		0
17,500																		1
Total	1	0	1	9	7	13	16	21	19	19	13	16	7	4	5	3	1	160

$$r = -0.023 \pm 0.051$$

TABLE XIX.—Correlation between the percentage of fat in cow's milk and the yield—Registered Ayrshires 5 years and over

	Percentage of fat																	Total.
	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	
8,500.....						2	8	4	4	5			1				1	25
9,000.....		1	2		7	9	10	3	10	3	5	5	5	2			1	62
9,500.....			3	5	6	9	5	9	4	3	4	6	1		1		1	37
10,000.....		1	0	3	3	2	10	10	5	1	1	5	1		1		1	50
10,500.....	1	1	5	2	1	9	7	3	6	5	2							42
11,000.....		3	2	4	3	7	6	5	5	4	2	1				1		47
11,500.....	1		1	2	2	4	2	4	3	2	1	4		1		1		28
12,000.....			1	2	1	3	4	2	4	2				1		1		20
12,500.....					3	3	5	3	5	1				1		1		20
13,000.....		1	2	2		1	3		1	2		1	1	1	1			15
13,500.....		1	1				1	2										5
14,000.....					1	1			3			1						6
14,500.....				1	1		1	1				1						5
15,000.....												1	1					2
15,500.....											1							4
16,000.....																		0
16,500.....							1											1
17,000.....				1						1								2
17,500.....																		0
18,000.....														1				1
18,500.....																		0
19,000.....																		0
19,500.....																		0
20,000.....								1										1
20,500.....																		0
21,000.....								1										1
21,500.....																		0
22,000.....									1									1
22,500.....																		0
23,000.....									1									1
Total.....	1	4	8	25	22	34	49	65	46	45	30	19	21	11	5	3	2	396

$$r_{\text{fat}} = -0.047 \pm 0.034$$

TABLE XX.—Correlation between the percentage of fat in cow's milk and the yield—Registered Ayrshires, all ages

[illegible] -0.138 ± 0.009

TABLE XXI.—Summary of results from a study of the correlation between percentage of fat and milk yield among different breeds of dairy cows

Breed and age.	Number of animals.	Milk.			Fat.			Correlation between percentages of fat and yield of milk.
		Mean.	Standard deviation.	Coefficient of variability.	Mean.	Standard deviation.	Coefficient of variability.	
Jersey, all ages.								
Jersey, 2 to 3 years.	877	6,475 ± 28.9	1,270 ± 120.5	19.61 ± 0.33	5,435 ± 0.012	0.171 ± 0.008	9.54 ± 0.15	-0.36 ± 0.030
Jersey, 3 to 4 years.	411	7,335 ± 43.8	1,377 ± 134.9	18.81 ± .40	5,403 ± .010	0.161 ± 0.013	10.41 ± .25	-0.47 ± .027
Jersey, 4 to 5 years.	210	8,043 ± 66.7	1,337 ± 134.9	16.83 ± .40	5,403 ± .010	0.161 ± 0.013	10.41 ± .25	-0.47 ± .027
Jersey, 5 years and over.	634	8,814 ± 43.1	1,068 ± 130.5	15.24 ± .35	5,374 ± .013	0.150 ± 0.010	9.44 ± .18	-0.397 ± .043
Jersey, all ages.	2,141	7,491 ± 28.0	1,178 ± 171.7	22.93 ± .35	5,393 ± .058	0.175 ± .005	9.74 ± .10	-0.344 ± .013
Guernsey, all ages.								
Guernsey, 2 to 3 years.	1,375	7,068 ± 28.8	1,584 ± 120.4	20.82 ± .77	5,065 ± .008	0.158 ± .006	9.01 ± .32	-0.31 ± .017
Guernsey, 3 to 4 years.	634	8,315 ± 45.9	1,584 ± 120.4	21.93 ± .40	5,065 ± .014	0.158 ± .010	9.13 ± .20	-0.30 ± .024
Guernsey, 4 to 5 years.	1,667	9,891 ± 43.8	2,087 ± 130.2	20.90 ± .63	4,950 ± .010	0.157 ± .007	9.64 ± .30	-0.317 ± .018
Guernsey, 5 years and over.	3,564	8,604 ± 23.7	2,095 ± 161.7	24.24 ± .20	5,013 ± .005	0.157 ± .004	9.35 ± .08	-0.296 ± .010
Guernsey, all ages.	7,100	8,604 ± 23.7	2,095 ± 161.7	24.24 ± .20	5,013 ± .005	0.157 ± .004	9.35 ± .08	-0.296 ± .010
Holstein-Friesian, all ages.								
Holstein-Friesian, 2 to 3 years.	610	12,433 ± 80.4	2,042 ± 161.8	23.56 ± .48	3,463 ± .008	0.204 ± .006	8.50 ± .16	-0.116 ± .027
Holstein-Friesian, 3 to 4 years.	341	13,935 ± 115.5	3,185 ± 181.4	22.87 ± .63	3,433 ± .012	0.204 ± .008	9.35 ± .24	-0.160 ± .030
Holstein-Friesian, 4 to 5 years.	692	14,585 ± 124.4	3,191 ± 161.9	21.23 ± .62	3,471 ± .012	0.211 ± .006	8.81 ± .16	-0.148 ± .024
Holstein-Friesian, 5 years and over.	1,995	14,443 ± 56.0	3,660 ± 130.6	25.27 ± .29	3,435 ± .005	0.205 ± .003	8.88 ± .10	-0.133 ± .020
Holstein-Friesian, all ages.	3,638	14,443 ± 56.0	3,660 ± 130.6	25.27 ± .29	3,435 ± .005	0.205 ± .003	8.88 ± .10	-0.133 ± .020
Ayrshire, all ages.								
Ayrshire, 2 to 3 years.	343	7,068 ± 43.9	1,314 ± 131.9	16.81 ± .44	4,016 ± .011	0.103 ± .008	7.71 ± .20	+0.09 ± .036
Ayrshire, 3 to 4 years.	343	9,170 ± 88.1	1,750 ± 160.9	19.28 ± .59	3,916 ± .014	0.103 ± .011	6.35 ± .28	-0.03 ± .034
Ayrshire, 4 to 5 years.	390	9,584 ± 83.5	1,566 ± 159.1	16.34 ± .61	3,916 ± .016	0.103 ± .011	7.73 ± .29	-0.03 ± .034
Ayrshire, 5 years and over.	1,091	10,726 ± 67.1	1,960 ± 147.5	18.40 ± .49	3,863 ± .011	0.103 ± .008	8.10 ± .19	-0.07 ± .034
Ayrshire, all ages.	1,091	9,417 ± 41.7	2,044 ± 139.5	21.71 ± .33	3,933 ± .008	0.103 ± .005	8.08 ± .13	-0.138 ± .020

CONTRIBUTION TO THE KNOWLEDGE OF TOXOPTERA GRAMINUM IN THE SOUTH

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INTRODUCTION

Although the spring grain aphid (*Toxoptera graminum* Rondani) has been treated fully in a bulletin¹ issued at a comparatively recent date by the United States Bureau of Entomology, the life-history studies mentioned therein were conducted primarily in the North, where sexual forms appear and the viviparous ones die off annually in the fall of the year. Comparatively little was known at the time of that publication of the life history of the species in the South, especially in the Southeast. Consequently the establishment of a field station at Columbia, S. C., afforded the senior writer a good opportunity to make a study of the insect in that section of the United States. This study was begun in the spring of 1913, continued through the year 1914, and to the spring of 1915. Its purpose was to ascertain whether or not *Toxoptera graminum* in that latitude breeds viviparously throughout the year, and, if so, (a) for how long a period it breeds in this manner, (b) whether or not the strain becomes weaker as it gets older, and (c) whether or not sexual forms are produced.

In addition to this study a number of molting experiments were conducted during the spring and summer months of 1914 in order that the variations in the duration of instars as caused primarily by temperature conditions might be learned.

During the year 1914 the senior writer was assisted in conducting the experiments by the junior writer, and during the former's absence in the fall of that year the latter took charge of the work.

METHOD OF PROCEDURE

The breeding of series of generations began in March, 1913, with an individual taken from the field. The first-born of this individual was isolated as was the first-born of this and each succeeding generation in this series. A careful record was made of their progeny and of the length of life of the individuals constituting the generations. Similarly, a specimen and a record were kept of the last-born of the individual collected, and of the last-born of every succeeding generation originating in this series. The series collectively will be known in this paper as the "A" series.

¹ WHISTLER, F. M., and PHILLIPS, W. J. THE SPRING GRAIN APHID OR "GREEN BUG." U. S. Dept. Agr. Bur. Ent. Bul. 110, 153 p., 9 pl., 48 fig., 5 diag. 1912.

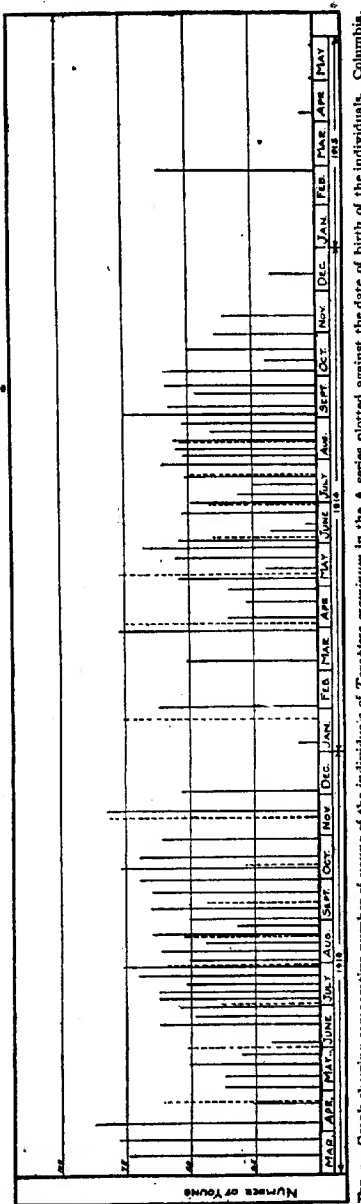


FIG. 1.—Graph showing comparative number of young of the individuals of *Toxoptera graminum* in the A series plotted against the date of birth of the individuals. Columbia, S. C., March 14, 1913, to June 9, 1915. Solid lines represent the young of the first-born and broken lines the young of the last-born individuals.

In the spring of 1914, after the A series had been running for one year, fresh series of first-born and last-born individuals were begun from an individual taken from the field, and similar records made as to the length of life and number of young of the individuals constituting the generations. These series, called the "B" series, were continued until the spring of 1915, or almost one year, after which they were discontinued and other fresh series started similar to the B series of the preceding year. These series, known as the C series, were continued until the A series gave out completely.

The purpose of conducting the B series and C series was to solve part "b" of the problem by comparing results with those obtained in the A series.

APPEARANCE OF OVIPAROUS FORMS

No oviparous forms appeared during the first year the experiments were in progress, the species breeding viviparously throughout that winter (1913-14).

In the fall of the second year, however, all the last-born individuals of the seventeenth generation developed into oviparous females. One individual of the line of generations of those last born in the B series in the late fall of 1914 also

developed into an oviparous female. From one of the oviparous forms in the A series a number of eggs were obtained but these eggs were infertile

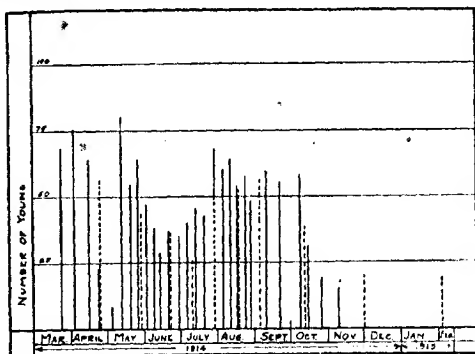


FIG. 2.—Graph showing the comparative number of young of the individuals of *Toxoptera graminum* in the B series plotted against the date of birth of the individuals. Columbia, S. C., March 23, 1914, to April 26, 1915. Solid lines represent the young of the first-born and broken lines the young of the last-born individuals.

as no males had developed in any of the cages and none could be found in nature. The females lived for about one month. It seems entirely

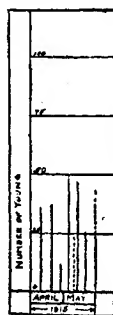


FIG. 3.—Graph showing comparative number of young of the individuals of *Toxoptera graminum* in the C series plotted against the date of birth of the individuals. Columbia, S. C., April 10, 1915, to June 26, 1915. Solid lines represent the young of the first-born and broken lines the young of the last-born individuals.

individual gave birth to 82 young, the reproductive period in this case

probable that if fertile eggs had been obtained they would have hatched either during warm days in winter or early the following spring. According to Webster and Phillips,¹ it is necessary for the eggs to be subjected to cold weather and freezes to make hatching possible. Freezes occur in the latitude of Columbia, S. C., although they are not so severe as are those in the region where the species was studied by Mr. Phillips; yet it seems possible that they were sufficiently severe to meet conditions necessary for the hatching of these eggs.

COMPARATIVE NUMBER OF YOUNG OF INDIVIDUALS IN THE DIFFERENT SERIES

A comparison of the number of young of the individuals in the different series is shown in figures 1 to 3. The solid lines in these diagrams represent the young of the first-born and the broken lines the young of the last-born individuals. The largest number of young born from any individual in the A series was 88, the reproductive period being only 22 days. This individual was born during the month of April, 1913. During the following winter another

¹ WEBSTER, F. M., and PHILLIPS, W. J. OP. CIT.

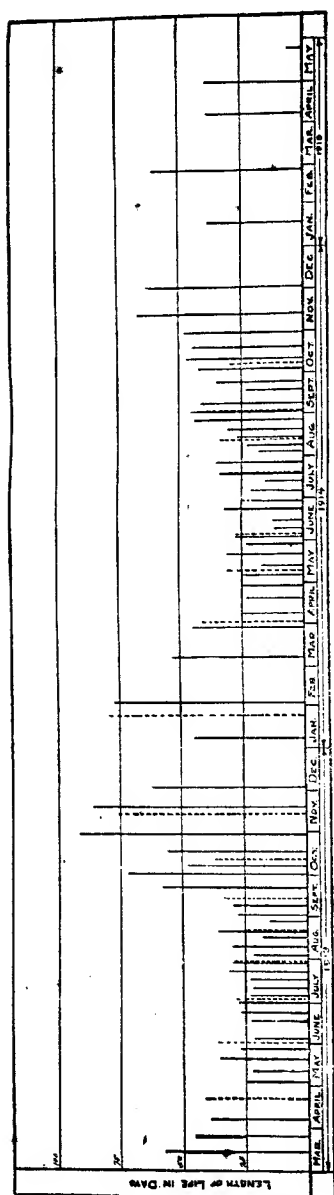


FIG. 4.—Graph showing comparative length of life of individuals of *Trialeurodes graminum* in the A series plotted against the date of birth of the individuals, Columbia, S. C., March 14, 1913, to June 9, 1915. Solid lines represent first-born and broken lines last-born individuals.

being 60 days. This female was born about the middle of November (1913) and lived until almost the middle of the following February (1914). The low level in reproduction in this series was reached during the summer months. The average number of young produced during these months is only about half that produced in early spring or late fall. Figure 1 shows further that the average number of young of the individuals during the first year was greater than the number produced from the individuals in the second year. This would seem to indicate a weakening of the strain. If, however, the average number of young produced during the second year in the A series is compared with the average number produced in the B series during the same period it will be noted that there were more young in the former series than in the latter. If the number of young aphids during the spring of the third year in the A series be compared with those in the C series during the same period it will be seen that there were more young in the latter series than in the former.

The female representing the seventy-first generation of first-born individuals in the A series died without producing young.

COMPARATIVE LENGTH OF LIFE OF INDIVIDUALS IN THE DIFFERENT SERIES

The length of life of individuals constituting the generations in the different series is clearly represented in figures 4, 5, and 6. In these

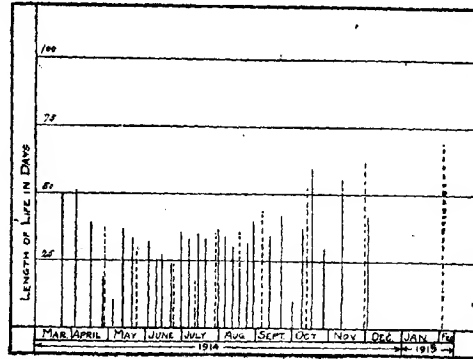


FIG. 5.—Graph showing comparative length of life of the individuals of *Toxoptera graminum* in the B series plotted against the date of birth of the individuals. Columbia, S. C., March 23, 1914, to April 26, 1915. Solid lines represent generations of first-born and broken lines generations of last-born individuals.

diagrams the heavy solid lines represent first-born individuals and the broken ones last-born individuals. By referring to figure 4 it will be

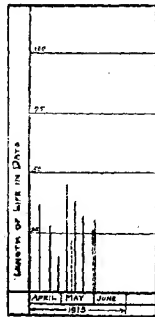


FIG. 6.—Graph showing comparative length of life of individuals of *Toxoptera graminum* in the C series plotted against the date of birth of the individuals. Columbia, S. C., April 10, 1915, to June 26, 1915. Solid lines represent generations of first-born and broken lines generations of last-born individuals.

seen that the life of individuals born during the months of May, June, July, and August was much shorter than of those born during the following four months; in fact, the individuals born during summer lived only about one-half as long as those born during fall. The longest-lived individual in this series was born during the latter part of October and lived for a period of about three months. The individuals born during the summer months of the second year in the A series were shorter lived than were those born during the same months the preceding year in the same series. Similarly the individuals born during the fall and early winter of 1914 were also shorter lived than were those born during the same period in the preceding year in this series. This fact would seem to indicate that the strain became weaker the second year, and this presumption is supported further by the results obtained from the control experiments conducted during the year 1914, known as the B series. By comparing the individuals in the A series with those of the B series it will be noted

that the life of those in the former series was shorter than that of those in the latter, the difference, however, not being very great. And if the individuals in the A series during the spring of 1915, the third year of the experiment, are compared with the individuals in the C series it will be noted that the average length of life is also somewhat less in the A series than in the C series. An adequate comparison, however, is difficult here, as there were fewer individuals in the former than in the latter series. In fact, there were only three first-born individuals in the A series as compared with eight first-born in the C series.

NUMBER OF GENERATIONS PER YEAR

A maximum of 33 generations of first-born individuals was obtained in the A series during the first year and a minimum of 9 generations of last-born individuals, making approximately 21 generations for the year. The following year (1914) a maximum of 21 first-born generations was reared and a minimum of 7 generations was reared until September, when the last generation gave rise to oviparous females.

The total number of generations for the whole series, as will be noted by referring to Table I, was 71 of the first-born and 18 of the last-born individuals.*

TABLE I.—First and last born generations, date of birth, reproductive period in days, daily average and total number of young, total length of life, and maximum and minimum temperature during which each generation of *Toxoptera graminum* lived. Columbia, S. C., 1913-1915

SERIES A

Generations.				Reproductive period.	Young.		Length of life.	Temperature.	
First-born.	Last-born.	Dates.			Daily average.	Total.		Maximum.	Minimum.
		1913.	1913.	* Days.			Days.	* F.	* F.
1	Mar. 14 to May 11..	28	2.64	74	58	93	42	
2	26 to 11..	33	2.33	77	46	93	42	
3	Apr. 7 to 16..	22	4.09	88	39	93	42	
4	21 to 7..	4	6.50	26	16	93	42	
5	22 to June 2..	32	1.28	61	41	97	42	
6	May 3 to May 28..	15	2.46	37	25	93	51	
7	10 to June 2..	14	2.64	37	23	97	51	
8	19 to 27..	24	2.12	51	39	98	47	
9	27 to 23..	17	1.36	30	27	98	47	
10	3 June 1 to July 7..	25	2.08	52	36	100	47	
11	4 to June 26..	6	3.00	18	22	98	47	
12	17 to July 10..	15	4.13	62	23	100	65	
13	23 to 20..	17	2.82	48	27	100	65	
14	30 to 28..	20	2.75	55	28	102	65	
15	4 July 2 to Aug. 3..	22	1.72	38	32	102	65	
16	5 to July 28..	17	3.64	62	23	102	65	
17	10 to Aug. 1..	15	4.13	62	22	102	69	
18	16 to 8..	14	3.71	52	23	102	67	
19	22 to 23..	15	4.66	70	32	96	66	
20	28 to 27..	16	4.75	76	30	96	61	
21	5 Aug. 2 to 27..	16	3.68	59	29	96	61	
22	29 to 24..	12	4.25	51	22	95	61	
23	1 Aug. 8 to Sept. 7..	17	3.58	61	30	95	61	
24	15 to 2..	13	3.48	44	18	93	61	

* This table contains only the data for Series A.

* This table is really a summary of one the writers have prepared showing the date of first and last young, daily production, and maximum and minimum daily temperatures, along with other data given here, but owing to its large size it could not be included with this paper.

TABLE I.—First and last born generations, date of birth, reproductive period, in days, daily average and total number of young, total length of life, and maximum and minimum temperature during which each generation of *Toxoptera graminum* lived. Columbia, S. C., 1913-1915—Continued

SERIES A—continued

Generations.			Reproductive period.	Young.		Length of life.	Temperature.	
First-born.	Last-born.	Dates.		Daily average.	Total.		Maximum.	Minimum.
		1913. 1913.	Days.			Days.	* F.	* F.
21	6	Aug. 20 to Sept. 25..	21	3.04	64	36	93	48
		21 to 15..	18	2.88	52	25	93	56
22		27 to 11..	10	3.20	32	15	93	61
23		Sept. 1 to 29..	20	2.50	50	28	92	48
24		8 to Oct. 8..	21	3.14	66	30	91	48
	7	13 to 10..	21	2.04	43	33	88	47
25		20 to Nov. 17..	32	2.00	64	58	86	26
26		29 to Dec. 10..	42	1.66	69	72	86	24
27		Oct. 7 to Nov. 24..	46	1.71	77	48	85	28
	8	10 to 15..	26	1.07	28	36	85	26
28		16 to Dec. 11..	41	1.68	69	56	78	24
		1914.						
29		Oct. 29 to Jan. 30..	52	1.16	61	93	78	24
	9	Nov. 14 to 28..	62	1.30	81	75	78	24
30		18 to Feb. 12..	60	1.36	82	86	78	24
31		Dec. 3 to 3..	53	1.01	54	62	74	21
		1914.						
32		Jan. 7 to Feb. 21..	17	.47	8	45	74	24
	10	24 to Apr. 13..	23	3.30	76	79	78	21
33		Feb. 2 to 20..	41	1.51	62	77	84	21
34		Mar. 7 to 29..	23	2.26	52	53	92	29
35		28 to May 12..	29	3.03	78	45	92	40
	11	Apr. 3 to 14..	27	2.74	74	41	92	40
36		7 to 2..	10	3.50	35	25	92	40
37		19 to 12..	8	3.50	28	23	92	40
38		28 to 23..	16	2.18	35	25	93	52
39		May 6 to 30..	14	3.85	54	24	93	52
	12	9 to June 8..	22	3.50	77	30	96	52
40		13 to May 30..	4	5.00	20	17	99	55
41		21 to June 21..	13	4.38	56	31	99	56
42		20 to 20..	17	4.11	70	23	99	61
43		June 2 to 29..	14	3.85	54	27	103	60
	13	5 to July 2..	17	2.35	40	27	103	60
44		9 to June 21..	12	1.50	18	12	98	60
45		14 to 26..	2	1.50	3	12	103	60
46		22 to July 25..	20	2.65	53	33	103	62
47		29 to 20..	39	1.25	49	21	98	62
	14	29 to 23..	16	2.62	42	24	98	62
48		July 6 to 27..	13	2.38	31	21	102	67
49		13 to 28..	7	3.56	25	15	102	61
50		19 to Aug. 22..	17	3.05	52	34	102	61
	15	20 to 19..	19	2.57	49	30	102	61
51		27 to 31..	17	3.64	62	35	98	68
52		Aug. 3 to 21..	13	4.00	52	18	93	68
53		8 to 31..	15	3.66	55	23	94	69
	16	13 to Sept. 16..	15	3.53	53	34	94	63
54		14 to 9..	12	4.66	56	26	94	39
55		20 to 19..	23	1.78	41	30	94	60
56		27 to Oct. 10..	20	2.60	52	44	94	39
57		Sept. 2 to 17..	16	4.50	74	45	94	39
	17	3 to 12..	23	1.86	43	39	94	39
58		8 to 19..	17	4.00	68	41	94	33

TABLE I.—First and last born generations, date of birth, reproductive period in days, daily average and total number of young, total length of life, and maximum and minimum temperature during which each generation of *Toxoplasma graminum* lived. Columbia, S. C., 1913-1915—Continued

SERIES A—continued

Generations.			Reproductive period.	Young.		Length of life.	Temperature.	
First-born.	Last-born.	Dates.		Daily average.	Total.		Maximum.	Minimum.
		1914. 1914.	Days.			Days.	° F.	° F.
59	Sept. 17 to Oct. 10..	16	2.68	47	23	88	51
60	23 to 28..	24	2.45	59	35	86	34
61	Oct. 3 to Nov. 14..	28	2.35	66	42	86	34
	a 18	8 to 6..	0	.00	0	29	86	34
62	10 to 26..	6	3.33	20	47	86	51
63	19 to Dec. 2..	32	1.56	50	44	81	22
64	30 to 17..	28	1.42	40	48	81	21
		1915.						
65	Nov. 12 to Jan. 18..	41	.92	37	67	75	21
66	Dec. 2 to Feb. 3..	14	1.28	18	63	65	21
		1915.						
67	Jan. 18 to Feb. 26..	1	2.00	2	39	72	27
68	Feb. 25 to Apr. 27..	20	3.10	62	61	89	30
69	Apr. 7 to May 16..	16	.37	6	39	92	44
70	30 to June 9..	1	1.00	1	40	93	56
71	May 25 to May 31..	0	.00	0	6	93	58

SERIES B

		1914. 1914.						
1	Mar. 23 to May 12..	25	2.72	68	50	92	31
2	Apr. 3 to 24..	23	3.30	76	51	96	37
3	16 to 25..	23	2.73	63	39	96	40
4	26 to 15..	10	2.30	23	19	92	52
	2	27 to June 3..	21	2.66	56	37	96	52
5	May 4 to May 15..	2	4.00	8	11	92	52
6	12 to June 18..	16	5.00	80	37	99	55
7	20 to 21..	25	2.16	54	33	99	55
8	26 to 29..	14	4.57	64	34	103	60
	3	29 to 26..	11	4.00	44	28	103	60
9	June 2 to July 9..	18	2.60	47	37	103	60
10	8 to 3..	8	4.75	38	25	103	60
11	13 to 11..	20	1.45	29	28	103	60
12	21 to 15..	9	4.11	37	24	103	62
	4	22 to 16..	15	2.40	36	24	103	62
13	29 to Aug. 4..	27	1.29	35	36	100	61
14	July 6 to 8..	22	1.81	40	33	102	61
	5	11 to July 29..	9	2.88	26	18	102	67
15	13 to Aug. 17..	25	1.80	45	35	102	61
16	20 to 23..	20	2.15	43	33	102	61
17	29 to Sept. 4..	28	2.42	68	37	94	68
	6	29 to 2..	16	3.00	48	35	94	68
18	Aug. 5 to 8..	22	2.50	60	34	94	66
19	11 to 10..	19	3.36	64	30	94	63
20	17 to 8..	15	3.53	53	22	94	63
	7	18 to 22..	13	4.00	52	35	94	39
21	24 to 25..	27	2.11	57	32	94	39
22	28 to Oct. 7..	26	1.84	48	40	94	39

a Oviparous female.

TABLE I.—First and last born generations, date of birth, reproductive period in days, daily average and total number of young, total length of life, and maximum and minimum temperature during which each generation of *Toxoptera graminum* lived. Columbia, S. C., 1913-1915—Continued

SERIES B—continued

Generations.			Reproductive period.	Young.		Length of life.	Temperature.	
First born.	Last born.	Dates.		Daily average.	Total.		Maximum.	Minimum.
		1914. 1914.	Days.			Days.	° F.	° F.
	8	Sept. 5 to Oct. 19..	28	2.00	56	44	94	39
23	11 to 15..	24	2.54	61	34	88	30
24	21 to Nov. 2..	34	1.61	55	42	86	40
25	30 to Oct. 10..	2	1.50	3	10	85	57
26	Oct. 8 to Nov. 14..	28	2.07	58	37	86	34
	9	12 to Dec. 3..	42	.90	38	52	84	22
27	15 to 14..	41	.76	31	60	81	22
28	26 to Nov. 24..	14	1.35	19	29	81	22
		1915.						
29	Nov. 10 to Jan. 5..	24	.66	16	56	70	21
	10	Dec. 1 to Feb. 4..	17	1.47	25	65	71	21
30	2 to Jan. 13..	0	.00	0	42	65	21
	*							
	11	1915. Feb. 3 to Apr. 13..	26	.73	19	69	83	27

SERIES C

		1915. 1915.						
1	Apr. 10 to May 17..	22	1.63	36	37	92	44
2	20 to 18..	19	1.94	37	28	92	54
3	28 to 13..	7	1.71	12	15	90	56
4	May 6 to June 20..	25	2.20	55	45	95	56
	2	11 to 2..	15	1.60	24	22	93	56
5	14 to 21..	23	2.04	47	38	95	56
6	21 to 21..	15	1.73	26	31	95	56
7	31 to 30..	15	1.60	24	30	95	56
	3	31 to 26..	18	2.44	44	26	95	56

VARIATIONS IN DURATION OF INSTARS AS AFFECTED PRIMARILY BY TEMPERATURE CONDITIONS

Temperature conditions play an important rôle in the duration of instars in *Toxoptera graminum*. To ascertain the exact variation in length of instars a series of molting experiments was conducted in 1914 during the months of March, April, May, June, and August. It was intended that a series should be conducted every month for one whole year, but other pressing work prevented this. Enough data, however, have been gathered from the experiments actually carried on to show the positive influence of this factor.

By referring to Table II it will be seen that there was a gradual decrease in the length of individual instars from March to August, the instars in March having been from two to three times as long as those in August.

TABLE 11.—Duration of instars of *Toxoptera graminum*, Columbia, S. C., 1914

Born.	Date of first molt.	Period between first and second molt.	Date of second molt.	Period between second and third molt.	Date of third molt.	Period between third and fourth molt.	Date of fourth molt.	Period between fourth and fifth molt.	Entire immature period (approximate).
1914.									
May 12, 2 p. m.	Mar. 16, 3 p. m.	66	Mar. 16, 3 p. m.	108	Mar. 25, 11 a. m.	117	Mar. 28, 12 noon	71	Hours.
12, 2 p. m.	16, 3 p. m.	66	16, 3 p. m.	108	28, 1 p. m.	117	28, 1 p. m.	71	384
12, 2 p. m.	16, 3 p. m.	66	16, 3 p. m.	108	28, 1 p. m.	117	28, 1 p. m.	71	384
12, 2 p. m.	16, 3 p. m.	66	16, 3 p. m.	108	28, 1 p. m.	117	28, 1 p. m.	71	384
12, 2 p. m.	16, 3 p. m.	66	16, 3 p. m.	108	28, 1 p. m.	117	28, 1 p. m.	71	384
12, 2 p. m.	16, 3 p. m.	66	16, 3 p. m.	108	28, 1 p. m.	117	28, 1 p. m.	71	384
12, 2 p. m.	16, 3 p. m.	66	16, 3 p. m.	108	28, 1 p. m.	117	28, 1 p. m.	71	384
12, 2 p. m.	16, 3 p. m.	66	16, 3 p. m.	108	28, 1 p. m.	117	28, 1 p. m.	71	384
12, 2 p. m.	16, 3 p. m.	66	16, 3 p. m.	108	28, 1 p. m.	117	28, 1 p. m.	71	384
12, 2 p. m.	16, 3 p. m.	66	16, 3 p. m.	108	28, 1 p. m.	117	28, 1 p. m.	71	384
Average.		96		112		131.5		62.84	402.13
1915.									
Apr. 2, 3 p. m.	Apr. 5, 3 p. m.	72	Apr. 8, 9 a. m.	66	Apr. 12, 12 noon	99	Apr. 14, 2 p. m.	50	287
2, 3 p. m.	5, 3 p. m.	72	8, 9 a. m.	66	12, 12 noon	99	14, 2 p. m.	50	287
2, 3 p. m.	5, 3 p. m.	72	8, 9 a. m.	66	12, 12 noon	99	14, 2 p. m.	50	287
2, 3 p. m.	5, 3 p. m.	72	8, 9 a. m.	66	12, 12 noon	99	14, 2 p. m.	50	287
2, 3 p. m.	5, 3 p. m.	72	8, 9 a. m.	66	12, 12 noon	99	14, 2 p. m.	50	287
2, 3 p. m.	5, 3 p. m.	72	8, 9 a. m.	66	12, 12 noon	99	14, 2 p. m.	50	287
2, 3 p. m.	5, 3 p. m.	72	8, 9 a. m.	66	12, 12 noon	99	14, 2 p. m.	50	287
2, 3 p. m.	5, 3 p. m.	72	8, 9 a. m.	66	12, 12 noon	99	14, 2 p. m.	50	287
2, 3 p. m.	5, 3 p. m.	72	8, 9 a. m.	66	12, 12 noon	99	14, 2 p. m.	50	287
2, 3 p. m.	5, 3 p. m.	72	8, 9 a. m.	66	12, 12 noon	99	14, 2 p. m.	50	287
Average.		84.50		66.33		98.83		62.11	399
1916.									
May 8, 2 p. m.	May 11, 9 a. m.	67	May 12, 5 p. m.	32	May 14, 12 noon	43	May 16, 12 noon	48	190
8, 2 p. m.	11, 9 a. m.	67	12, 5 p. m.	32	14, 12 noon	43	16, 12 noon	48	190
8, 2 p. m.	11, 9 a. m.	67	12, 5 p. m.	32	14, 12 noon	43	16, 12 noon	48	190
8, 2 p. m.	11, 9 a. m.	67	12, 5 p. m.	32	14, 12 noon	43	16, 12 noon	48	190
8, 2 p. m.	11, 9 a. m.	67	12, 5 p. m.	32	14, 12 noon	43	16, 12 noon	48	190
8, 2 p. m.	11, 9 a. m.	67	12, 5 p. m.	32	14, 12 noon	43	16, 12 noon	48	190
8, 2 p. m.	11, 9 a. m.	67	12, 5 p. m.	32	14, 12 noon	43	16, 12 noon	48	190
8, 2 p. m.	11, 9 a. m.	67	12, 5 p. m.	32	14, 12 noon	43	16, 12 noon	48	190
8, 2 p. m.	11, 9 a. m.	67	12, 5 p. m.	32	14, 12 noon	43	16, 12 noon	48	190
8, 2 p. m.	11, 9 a. m.	67	12, 5 p. m.	32	14, 12 noon	43	16, 12 noon	48	190
Average.		68.30		35.40		38.40		62.11	203
1917.									
June 12, 2 p. m.	June 15, 8 a. m.	42	June 16, 3 p. m.	31	June 18, 3 p. m.	48	June 20, 8 a. m.	41	166
12, 2 p. m.	15, 8 a. m.	42	16, 3 p. m.	31	18, 3 p. m.	48	20, 8 a. m.	41	166
12, 2 p. m.	15, 8 a. m.	42	16, 3 p. m.	31	18, 3 p. m.	48	20, 8 a. m.	41	166
12, 2 p. m.	15, 8 a. m.	42	16, 3 p. m.	31	18, 3 p. m.	48	20, 8 a. m.	41	166
12, 2 p. m.	15, 8 a. m.	42	16, 3 p. m.	31	18, 3 p. m.	48	20, 8 a. m.	41	166
12, 2 p. m.	15, 8 a. m.	42	16, 3 p. m.	31	18, 3 p. m.	48	20, 8 a. m.	41	166
12, 2 p. m.	15, 8 a. m.	42	16, 3 p. m.	31	18, 3 p. m.	48	20, 8 a. m.	41	166
12, 2 p. m.	15, 8 a. m.	42	16, 3 p. m.	31	18, 3 p. m.	48	20, 8 a. m.	41	166
12, 2 p. m.	15, 8 a. m.	42	16, 3 p. m.	31	18, 3 p. m.	48	20, 8 a. m.	41	166
12, 2 p. m.	15, 8 a. m.	42	16, 3 p. m.	31	18, 3 p. m.	48	20, 8 a. m.	41	166
Average.		39.10		30.2		30.2		43.2	166

Aug. 22, 2 p. m.	43	Aug. 23, 3 p. m.	30	Aug. 26, 5 a. m.	26	Aug. 28, 3 p. m.	46	175
22, 2 p. m.	43	25, 9 a. m.	24	26, 2 p. m.	29	28, 8 a. m.	43	176
22, 2 p. m.	43	25, 32 NOON	27	29, 9 a. m.	43	31, 9 a. m.	43	178
22, 2 p. m.	43	27, 9 a. m.	27		43			211
Average	39-35		43		37-00		39-75	158-00

Mean temperature:

°F.

Mar. 12 to Mar. 29	53.1+
Apr. 3 to Apr. 16	58.9+
Apr. 16 to May 1	62.5+
May 1 to May 15	70.6+
June 21 to June 29	75.6+
Aug. 22 to Aug. 31	81.2

* All references to clock time refer to standard time.

The relation between temperature and immature stages is still more clearly brought out by comparing the average length of the immature stages of each series with the average mean temperature of the period during which each series was conducted. This comparison is well illustrated in figure 7. By referring to this diagram it will be noted that there was a marked shortening in the length of the immature period as the temperature of each month became higher until the month of June was reached. The length of the immature period in August was about the same as that for June when the temperature was becoming higher.

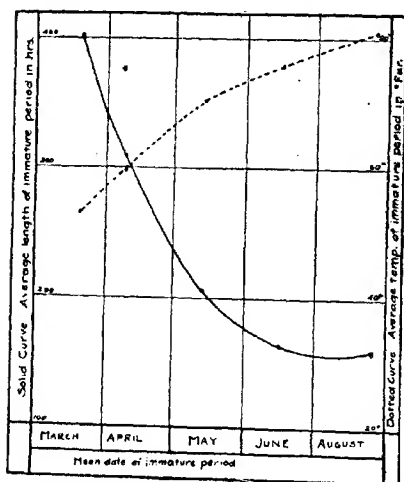


FIG. 7.—Graph showing effects of temperature upon length of immature period of *Toxoptera graminum*, plotted against the mean date of the immature period.

August and the temperature curve a downward course, the two curves crossing later on in the fall of the year.

In figure 8 the length of the immature period of the individuals is plotted against the mean temperature for the period during which the experiments were in progress.

REARING METHODS

In conducting the life-history studies of this species 6-inch flowerpot cages supplied with lantern chimneys covered with cheesecloth were utilized. Oats were used as host plants throughout the year. These cages were all kept under normal conditions throughout the year in an outdoor breeding shelter (Pl. 12, A). The curtains of this shelter were partly raised during sunny days to admit the warm sun's rays. Care was taken, however, that the rays did not strike the chimney covers as

The temperature curve and immature-period curve crossed in April. From this we may conclude that the length of the immature period is markedly affected until a certain point is reached, after which a higher temperature apparently has little or no effect in shortening the length of this period.

It is quite probable that had the experiments been carried on as originally planned, the immature-period curve would show an upward course after

this would have raised the temperature and produced abnormal conditions. At night and during cool, blustery days the curtains were lowered. An interior view of the shelter is shown in Plate 12, B. The arrow on the left of the figure points to the *Toxoptera* cages.

In conducting molting experiments it was found that a smaller type of cage than that used for line breeding gave best results. Three-inch flowerpots supplied with toy-lantern globes covered over with cheesecloth proved very satisfactory. Owing to the small size of these cages there was less chance for the individuals to get lost. Black fiber paper, such as is used in picture framing, was placed in the bottom of the cages, and this assisted very greatly in detection of the molted skins, which, being whitish, were conspicuous against the dark background.

CONCLUSION

Although valuable information on the life history of this species in the South has been obtained from these studies, further work is necessary to prove conclusively all the questions raised. One point has been proved in these investigations, and that is that oviparous forms develop in the latitude of Columbia, S. C. Whether or not the strain becomes weaker as it grows older requires further experimentation before we may be at all certain regarding it. The foregoing experiments would indicate this; yet it was found that insufficient control experiments had been conducted with the main series.

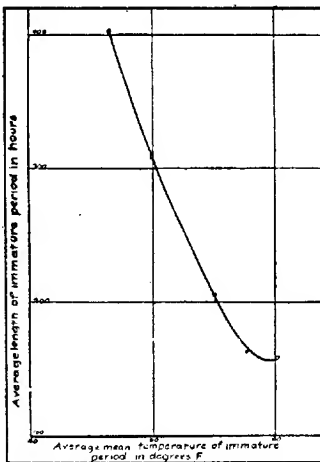


FIG. 8.—Same as figure 7, but in this diagram the average length of the immature period of *Toxoptera graminum* is plotted against the average temperature for that period.

PLATE 12

Toxoptera graminum

A.—Outdoor breeding shelter or insectary at Columbia, S. C., in which the cages were kept throughout the season.

B.—An interior view of the same. The arrow points to the cages used in rearing the insect.



CAN BIOLOGIC FORMS OF STEMRUST ON WHEAT CHANGE RAPIDLY ENOUGH TO INTERFERE WITH BREEDING FOR RUST RESISTANCE?¹

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COOPERATIVE INVESTIGATIONS BETWEEN THE AGRICULTURAL EXPERIMENT
STATION OF THE UNIVERSITY OF MINNESOTA AND THE BUREAU OF PLANT
INDUSTRY OF THE UNITED STATES DEPARTMENT OF AGRICULTURE

INTRODUCTION

Doubt has often been expressed whether it is possible to breed cereals permanently resistant to rusts. The opinion is commonly held that either the newly developed resistant variety loses its resistant quality or that the particular rust in question adapts itself to the new variety. The fundamental facts ought to be known if breeding is to be successful.

There are two main possibilities, besides mutation, as far as the rust is concerned. It is possible to assume that a highly resistant variety may occasionally be weakly infected by the rust and that, as a result of its sojourn on the host, the rust acquires additional virulence, thus enabling it to infect the variety with progressively greater ease. If this assumption be true, the degree of virulence of a rust on a particular cereal variety should be directly proportional to the length of its association with that variety, or a physiologically similar one. The second possibility is that the rust may be changed by a closely related host variety, species, or hybrid. That is, assume the presence in a breeding plot, or in a wider area, of varieties completely susceptible (S), moderately susceptible (S—), moderately resistant (R—), and highly resistant (R) to a given rust. The rust from S might not be able to pass directly to R, but might be able to pass to S—, thence to R—, and thence to R. S— and R— would therefore act as intermediaries or bridges between S and R. The rust having once grown on R could then continue to infect R.

If such hypothetical cases as cited above actually occur in nature, the value of breeding for rust resistance would be problematical. It was for this reason that the work reported in this paper was undertaken.

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² On leave.

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HISTORICAL REVIEW

Ward (11),¹ as a result of his extensive work with biologic forms of the rust of bromes (*Puccinia dispersa* Erikss.), first suggested the possible occurrence of bridging hosts. He suggested that bridging hosts might be hybrids or varieties taxonomically linking one predisposed species with another. Freeman (4) obtained results similar to Ward's. Salmon (7) concluded that biologic forms of *Erysiphe graminis* DC. on the genus *Bromus* might be broken down by the use of bridging hosts. Freeman and Johnson (5) and Johnson (6) obtained evidence that bridging hosts might also, in some cases, enable a biologic form of *P. graminis* Pers. to infect a host plant which was normally immune. Stakman (8) and Stakman and Piemeisel (9), on the other hand, could not get any evidence of bridging, nor of rapid changes in the parasitic capabilities of biologic forms of *P. graminis* Pers.

Although Ward first suggested the possible significance of hybrids in connection with bridging, Pole Evans (3) first called attention to the actual effect of such hybrids. He found that when immune and susceptible wheats were crossed, the resulting hybrid, whether infected naturally or artificially, was more susceptible to *Puccinia graminis* than the susceptible parent. In addition, he found that the rust from the hybrid was more virulent on the susceptible parent than the rust from that parent itself, and had even acquired the power to infect the immune parent. It therefore acted as a bridge between the susceptible parent and the immune parent, and intensified the action of the rust on the susceptible parent. The significance of these results is obvious, and if they were of universal application the outlook for breeding and successfully growing rust-resistant wheats would be discouraging.

Biffen (1) had previously shown resistance in wheats to the yellow-rust *Puccinia glumarum* Erikss. and Henn. to be a recessive Mendelian character and found that the relatively immune forms bred true. After the publication of Pole Evans's results, Biffen (2) published the results of extensive experiments, showing that F_2 individuals resulting from crossing susceptible and immune wheats show definite segregation. An analysis of the F_2 plants proved that 25 per cent of the individuals were relatively immune. These bred true, at least from 1907 to 1911. Some of the susceptible forms bred true, while others produced offspring which segregated into immune and susceptible forms in the ratio 1 to 3. Biffen also states that some of the susceptible F_2 plants are more susceptible than the susceptible parent, but that even if plants of the F_1 generation can act as a bridge between the susceptible and immune forms, the effects in the field are negligible. In support of his statement he points to the facts that the immune parents remained practically rust-free for eight seasons, even when growing near F_1 plants of resistant

¹ Reference is made by number (italic) to "Literature cited," p. 122-123.

and susceptible parentage, and that such sharp 3 to 1 segregation could not occur in the F_2 generation if plants with the constitution RR similar to that of the immune parent could be infected by rust from the DR plants. His F_2 resistant plants were still as resistant as those of the F_2 generation. He directs attention to the fact that Rivet wheat, one of the oldest English varieties, is still resistant to *P. glumarum*, and that einkorn, possibly the first wheat to be cultivated, is still resistant to most rusts. He concludes that if varieties lose their immunity, either on account of some change in their own nature or on account of increased virulence of the rust, the change is too slow to affect the work of plant breeders.

EXPERIMENTAL METHODS

In the experiments with *Puccinia graminis tritici-compacti*, unless otherwise specified, the grains used were Haynes Bluestem wheat, (Minnesota 169, *Triticum vulgare*); Manchuria barley (Minnesota 105, *Hordeum vulgare*); Swedish rye (Minnesota 2, *Secale secale*); and Improved Ligova oats (Minnesota 281, *Avena sativa*). The methods used were similar to those described by Stakman and Piemeisel (10, p. 431-432).

In estimating the degree of infection, more significance was attached to the character than to the number of uredinia. The total number of uredinia produced is no adequate index of resistance unless the size be considered together with flecking or yellowing of the leaf. All the inoculated leaves of a highly resistant variety often become infected, but the character of infection is quite different from that in a susceptible variety.

On resistant varieties the uredinia are usually smaller, less confluent, and are usually surrounded by a more or less definite yellowed or whitened area, while the uredinia on susceptible plants produce more spores, become larger, and tend to coalesce. This difference is shown clearly in Plate 14, in which A and B show a susceptible form, while C and D represent a partly resistant variety. The differences between the susceptible Marquis shown at B, Plate 16, and the resistant Kubanka shown at C and D may appear indistinct at first glance; but close observation shows clearly the much more pronounced whitening of the tissues near the uredinia on the partly resistant Kubanka. Usually the uredinia on Marquis are larger than those shown in B, while those on the Kubanka at C and D are about normal. An almost immune form is shown at D and E, Plate 15.

The difference between moderately susceptible and completely susceptible hosts, such as that between club wheats infected with *P. graminis tritici-compacti* and barley infected with the same rust, may be shown in degree of infection only. Barley is infected fairly normally, but not so heavily as club wheats.

The wheat hybrids inoculated with *P. graminis tritici* included F_1 and F_2 generation plants, with those of resistant and susceptible parents for comparison, and in addition F_3 plants of a hybrid which was breeding true for the agronomic characters and showing partial resistance to stem rust. Seedlings of Bobs, one of the parent varieties of the cross described by Pole Evans (3), were also tested.

The F_1 plants were of the cross Haynes Bluestem (Minnesota 169; susceptible) \times Kubanka (CI¹ 2094; resistant). F_2 plants of two different crosses were used: White Spring emmer (Minnesota 1165; very resistant) \times Marquis (susceptible); and Marquis (susceptible) \times Kubanka (CI 2094; resistant). The F_3 plants were of the cross Haynes Bluestem (Minnesota 169; susceptible) \times Kubanka (CI 2094; resistant). Inoculation methods with seedlings were the same as those already referred to. The F_1 and F_2 hybrid plants, which served as sources for the material used to inoculate seedlings of the parent varieties, were inoculated at time of heading, placed in a large metal moist chamber for two days, then removed to the greenhouse bench.

RESULTS

Attempts were made to change the parasitic capabilities of *P. graminis tritici-compacti*, a new biologic form recently described by Stakman and Piemeisel (10), both by the use of what should theoretically be bridging hosts and by confining the rust for a period of time to an uncongenial host. This rust was selected on account of its action within the common-wheat group (*Triticum vulgare*). Most hard spring wheats, such as Haynes Bluestem, Fife (Minnesota 163), and Marquis, as well as many winter wheats of the Crimean group, are resistant, while most soft wheats, such as Early Baart, Dicklow, and Washington Bluestem, are quite susceptible, as are also the club wheats. The rust differs but little from *P. graminis tritici* except in its action on hard wheats of the *T. vulgare* group.² A number of grasses, barley, and club wheats are equally congenial hosts for both forms. It would seem that if *P. graminis tritici-compacti* could be induced to transfer normally to resistant hard wheats at all, one of the hosts common to both rust forms should act as an intermediary or bridge between the susceptible grass or wheat and the resistant hard wheat. Barley, which has been shown by Freeman and Johnson (5, p. 18) to act as a bridge for *P. graminis* between various cereals, was used in the expectation that it might act as a bridging host in this case also. The results are given in diagram 1.

EXPLANATION OF DIAGRAMS 1 TO 3

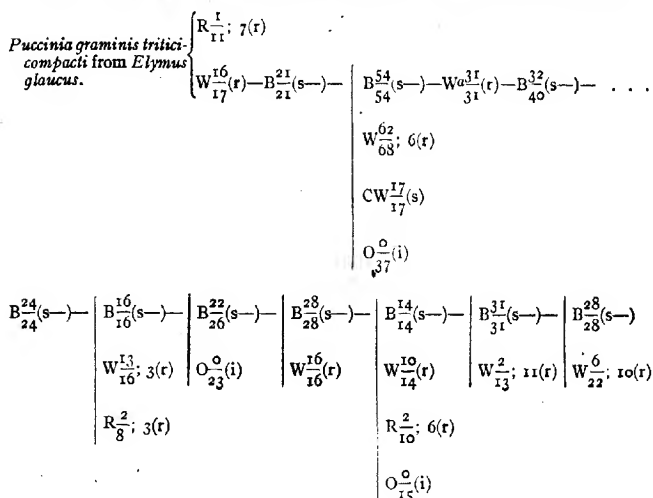
In diagrams 1, 2, and 3 wheat is represented by "W," barley by "B," club wheat by "CW," oats by "O," and rye by "R." Transfers are indicated by dashes; thus "W-B" means that the rust was transferred from wheat to barley and to all other cereals indicated in the same vertical column. The results of inoculations are given

¹ CI—Cereal Investigations No.

² See Stakman and Piemeisel (10, p. 468-470; Pl. 54, 55).

in the form of a fraction, the denominator indicating the total number of leaves inoculated and the numerator the number which became infected. The number of leaves which became distinctly flecked but did not develop uredinia, is given after the semicolon. The degree of susceptibility is indicated after each transfer as follows: (s), very susceptible; (s—), moderately susceptible; (r—), moderately resistant; (r), very resistant; (i), immune. Although the word "immune" is used, it is quite likely that oats may be very rarely, indeed, and very weakly infected.

DIAGRAM 1.—Effect of barley on the parasitic capabilities of *Puccinia graminis tritici-compacti*

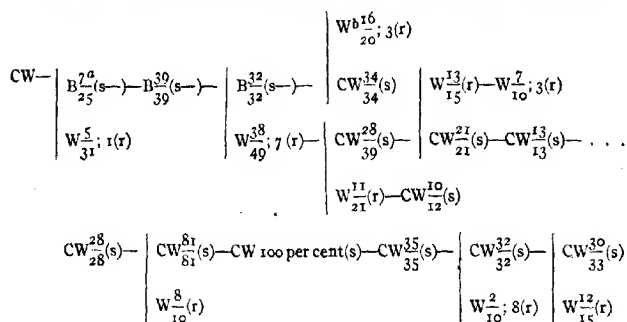


It will be seen from diagram 1 that club wheat and barley are susceptible to the rust, which develops normally on both, although it grows more luxuriantly on club wheat. It is equally clear that barley did not enable the rust to attack Haynes Bluestem wheat any more readily than it could before having been transferred to barley. The rust was confined to barley for seven successive "urediniospore generations" covering a period of four months, and at the end of that time it had not acquired any additional virulence whatever on wheat. The same is true of its action on oats and rye. Neither did it lose any virulence as a result of its sojourn on Marquis wheat on which it developed very weakly. Incidentally the results also showed that the rust did not adapt itself to more luxuriant development on barley, on account of its long association with it. As indicated, the rust does not develop as luxuriantly on barley as on club wheat, and it never acquired that ability. In this case at least barley does not act as an intermediary or bridging host.

* Marquis wheat.

Club wheat is also a host for both *P. graministritici* and *P. graminis tritici-compacti*. Theoretically, therefore, if bridging species really occur, this host might be expected to act as one on account of its close taxonomic relationship to the common wheats. When the *tritici-compacti* rust was found on club wheat in the field, therefore, inoculations were made on barley and wheat, and finally the rust was confined to club wheat for a period of about four months and transferred to wheat periodically. The results are given in diagram 2.

DIAGRAM 2.—Effect of club wheat on the parasitic capabilities of *Puccinia graminis tritici-compacti*



Club wheat did not change the rust at all; neither did the combination of barley and club wheat. As a matter of fact, one would scarcely expect club wheat to change the rust enough to enable it to attack wheat more easily, because it is found on club wheat in the field, and if this host changed the fungus it would not remain different from *P. graminis tritici*.

If neither barley nor club wheat enabled *P. graminis tritici-compacti* to parasitize common wheat more successfully, it would seem possible that some other species of *Triticum* or, more likely still, some susceptible variety of *T. vulgare* might bring about the desired result. Representatives of the different species of *Triticum* were inoculated, but none seemed to give particular promise. Some of the soft wheats of the *T. vulgare* group were found to be susceptible and the rust was transferred from them to hard wheats. The results were monotonously similar to those given in diagrams 1 and 2.

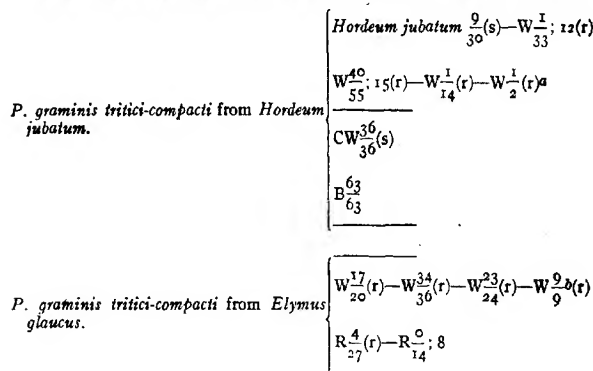
After all attempts failed with possible bridging hosts, the effect of successive transfers to wheat itself was next tried. If a closely related variety or species can suddenly and fundamentally change a rust so as to enable it to pass to a normally almost immune variety, it seems reasonable to suppose that, having once established itself on an almost immune

* Inoculations made a month after material was collected: consequently few spores germinated.

† File (Minnesota 163).

host, constant association with this host should increase its virulence. The results of trials to determine this are given in diagram 3.

DIAGRAM 3.—Results of successive transfers of *Puccinia graminis tritici-compacti* to resistant wheat.



There was no increase in virulence as a result of keeping the rust on wheat, the character of infection being the same at the end of the experiment as it had been at the beginning.²

The effect of hybrids on *P. graminis tritici* was next tried. The results are given in Tables I to V.

TABLE I.—Results of inoculations with *P. graminis tritici* on resistant and susceptible parents with rust from susceptible *F*₁ hybrid and from stock cultures on susceptible parent

Source of rust.	Plant inoculated.	Result.	Character of infection.
Stock cultures....	Haynes Bluestem..	$\frac{50}{50}$	Heavy; numerous, large uredinia.
<i>F</i> ₁ hybrid.....do.....	$\frac{47}{47}$	Do.
Stock cultures....	Kubanka 2094.....	$\frac{49}{49}$	Moderate; uredinia smaller, sharp flecks.
<i>F</i> ₁ hybrid.....do.....	$\frac{47}{47}$	Do.

The *F*₁ hybrid plant shown in Plate 13, B, furnished the spore material for the inoculations made on the seedling leaves of the parent varieties, Haynes Bluestem (Minnesota 169), and Kubanka (CI 2094). Normal

^a Uredinium too small to transfer.

^b For the character of infection of *P. graminis tritici-compacti* on Haynes Bluestem wheat (Minnesota 169) see Stakman and Pieneisel (10, Pl. 55, A).

uredinia appeared on leaf blades and sheaths, as well as on the fasciated glumes, and the plant was without doubt susceptible. The two series of inoculations, one from the stock cultures and the other from this hybrid plant, made on seedlings of Haynes Bluestem (Minnesota 169) gave similar results. In both series numerous uredinia appeared in the usual time and developed to normal size. There was, however, no evidence that Bluestem wheat was any more susceptible than when inoculated with rust from other plants of the same variety (Pl. 14, A, B).

Two series of inoculations made on seedlings of the somewhat resistant parent, Kubanka (CI 2094) also failed to reveal any differences in degree of infection resulting from the source of the inoculum. Although uredinia were formed on all leaves inoculated, many of them were smaller than those on the susceptible variety and sharp flecks were nearly always present, indicating at least some resistance. There was no evidence whatever that Kubanka (CI 2094) was more susceptible to the rust from the hybrid than to rust from any other source (Pl. 14, C, D).

TABLE II.—Results of inoculations with *P. graminis tritici* on resistant and susceptible parents with rust from susceptible F_2 hybrid and from stock cultures

Source of rust.	Plant inoculated.	Result.	Character of infection.
Stock cultures....	Marquis.....	$\frac{49}{49}$	Very heavy; large uredinia.
F_2 hybrid.....do.....	$\frac{51}{51}$	Do.
Stock cultures....	Emmer (Minn. 1165).	$\frac{0}{54}$	Nearly immune; no uredinia; very small, light green flecks.
F_2 hybrid.....do.....	$\frac{0}{61}$	Do.

Table II shows the results of inoculations with the rust from the F_2 hybrid, White Spring emmer (Minnesota 1165) \times Marquis, on seedlings of the two parent varieties, and furnishes the most convincing evidence that this particular susceptible hybrid does not increase the virulence of the rust for either parent variety. Normal uredinia on the hybrid plant shown at A in Plate 15, furnished the spore material used to inoculate the seedlings of susceptible Marquis and the extremely resistant emmer parents. On all the seedlings of Marquis, normal infection resulted, both from inoculations made with rust from stock cultures, and with those from the susceptible hybrid. There was no observable difference in number or size of uredinia. Neither were there any indications of resistance, nor of increased susceptibility in those plants inoculated

with rust from the hybrid (Pl. 15, B, C). A total of 115 seedlings of the remarkably resistant (nearly immune) emmer parent were inoculated, 54 with rust from stock cultures, and 61 with rust from the susceptible hybrid, but not a single uredinium was formed. Very small light-green flecks appeared, but never developed into uredinia. In so far as indicated by these experiments, this emmer may be described as "once resistant, always resistant" (Pl. 15, D, E).

TABLE III.—Results of inoculations with *P. graminis tritici* on resistant and susceptible parents with rust from susceptible F_2 hybrid and from stock cultures

[Marquis \times Kubanka (CI 2094)]			
Source of rust.	Plant inoculated.	Result.	Character of infection.
Stock cultures....	Marquis.....	55	Moderately heavy; large, vigorous uredinia.
		55	
F_2 hybrid.....do.....	47	Do.
		47	
Stock cultures....	Kubanka (CI 2094).	48	Moderate; uredinia smaller, flecks present.
		48	
F_2 hybrid.....do.....	52	Do.
		52	

Table III gives the results with the other F_2 hybrid [Marquis \times Kubanka (CI 2094)]. The F_2 plant from which urediniospores were used to inoculate seedlings of the two parents, is shown at A in Plate 16. Uredinia are present on leaf, sheaths, and glumes. The results were similar to those previously described (Pl. 16, B, C, D).

Having determined the effect of an F_1 hybrid, and two F_2 hybrids, it seemed advisable to try a hybrid of a later generation which was breeding true for such morphological characters as presence of awns, hairy chaff, durum-like shape of spike, etc. For this work, seed from the F_2 plants of the cross Haynes Bluestem (Minnesota 169) \times Kubanka (CI 2094) was chosen. Seedlings were grown, and 66 plants were inoculated with rust from the stock cultures and the resulting urediniospores were used to inoculate seedlings of the two parent varieties. The results are given in Table IV. The inoculations on this hybrid show that it is not yet homozygous for the character of rust resistance, even though it has for several years been breeding true for other characters. Here again, as in previous trials, a sojourn on the hybrid did not increase the virulence of the rust on either parent perceptibly (Pl. 17).

TABLE IV.—Results of inoculations with *P. graminis tritici* on resistant and susceptible parents and F_2 hybrid with rust from partially resistant F_2 hybrid and from stock cultures

Source of rust.	Plant inoculated.	Result.	Character of infection.
Stock cultures....	Hybrid 4 × 38AA....	$\frac{66}{66}$	Variable; uredinia large and numerous on some leaves, small and few on others. Some leaves show sharp flecking, others none.
Do.....	Haynes Bluestem....	$\frac{59}{59}$	Heavy
F_2 hybrid.....	do.....	$\frac{52}{52}$	Do.
Stock cultures....	Kuhanka 2094.....	$\frac{55}{55}$	Moderate; uredinia small, flecks present.
F_2 hybrid.....	do.....	$\frac{49}{49}$	Do.

GENERAL DISCUSSION

The results of the experiments with *P. graminis tritici-compacti* show that barley which both theoretically and from the results obtained by previous investigators might be expected to increase the infection range does not do so. Even susceptible varieties of wheat do not change the parasitic capabilities of the rust so as to enable it to attack a normally resistant variety. Furthermore, the rust does not acquire additional virulence when associated for a long time with a given host. Barley is moderately susceptible to the rust but the relations between host and rust are apparently the same regardless of the length of their association with each other. Wheats resistant to the rust remain resistant regardless of the previous history of the rust.

The results of the work to ascertain the effect of hybrids on *P. graminis tritici* are not at all in agreement with those of Pole Evans (3). Bobs, the wheat found to be immune under the conditions of his experiments, is quite susceptible under our conditions, both in the field-rust nursery and greenhouse (Pl. 13, A). Possibly the strain of rust in South Africa is not the same as ours.

On account of the far-reaching significance of Pole Evans's results, the utmost precautions were taken in the present work to detect any differences which might appear in either the resistant or susceptible parents when inoculated with rust from the hybrid as compared with that from stock cultures. In no case, however, was there the slightest evidence of any change in the virulence of the parasite, nor any indication that a short sojourn on a susceptible hybrid had given it any peculiar ability to cause normal infection on a heretofore resistant variety or to cause a more than usually virulent infection on a susceptible variety.

Observations in the rust nursery extending over a period of seven years also serve to strengthen the idea that rust resistance is a definite character present in a greater or less degree in particular varieties and not greatly influenced by cultural conditions. It has not been possible to build up resistance within a susceptible line by continuous selection nor to isolate resistant plants from such a line. Since 1915 several hundred varieties of all degrees of susceptibility and resistance have been grown in the same nursery with hybrids of the F_1 , F_2 , and later generations and always under optimum conditions for infection—that is, in a severe epiphytotic of stemrust. No instances have been observed of a resistant variety being attacked by a form of stemrust able to cause severe infection, as would be expected if the hybrid plants near by could produce such a rust form. There are seasonal fluctuations in the severity of the rust attack, but the greenhouse experiments here reported, the experimental work in the rust nursery, and the field observations in several States with resistant varieties of spring and winter wheats, and with oats, all point to the conclusion that both rust and host are relatively stable. It seems more likely that resistant varieties will be only of regional value because of the occurrence of different biologic forms in various regions.

There seems, however, no basis, from the facts now at hand, for the fear expressed by Pole Evans that these hybrids once produced will not only gradually lose their own power to resist attacks of the rust, but will also give the parasite new infection capabilities, enabling it to cause greater injury in susceptible varieties and even to attack previously resistant varieties.

SUMMARY

(1) Neither barley nor club wheat enabled *Puccinia graminis tritici-compacti* to attack resistant common wheats or other resistant cereals more vigorously than normally.

(2) *P. graminis tritici-compacti* was confined to barley and resistant wheat for a number of successive generations, but it did not acquire increased virulence for these hosts.

(3) The parasitism of *P. graminis tritici-compacti* was not changed by bridging hosts nor by association with a given host.

(4) *P. graminis tritici* was used to determine the possible action of hybrids as bridging forms. Studies were made of F_1 , F_2 , and F_3 hybrids in comparison with their resistant and susceptible parent varieties.

(5) Susceptible plants of the F_1 generation of the cross Haynes Bluestem (Minnesota 169) \times Kubanka (CI 2094) did not enable the rust to infect seedlings of the resistant parent normally, nor to infect the susceptible parent more virulently.

(6) The culture of stemrust on susceptible plants of the F_2 generation of the cross White Spring emmer (Minnesota 1165) \times Marquis had no appreciable effect on the parasite.

(7) Negative results were obtained in attempting to alter the infection capabilities of the rust by growing it for generation on susceptible F_2 plants of the cross Marquis \times Kubanka (CI 2094).

(8) F_2 hybrids of the cross Haynes Bluestem \times Kubanka (CI 2094) were apparently homozygous for morphological characters but heterozygous for the character of rust resistance. Susceptible hybrid plants did not act as bridges for the rust.

(9) The facts recorded in this paper, supported by experimental work in the rust nursery and by field observations, indicate that rust resistance is comparable with other permanent characters, and that it is not primarily controlled by seasonal conditions, soil type, geographical location, or other cultural conditions. It is rather an hereditary character, which can not be produced by the accumulation of fluctuating variations within a susceptible line, nor broken down by changes in the host or parasite.

(10) The resistance of wheat varieties may vary in different regions because of the presence of different biologic forms of rust.

(11) There seems to be little basis for the belief that hybrids between resistant and susceptible varieties will exert a harmful final effect by increasing the virulence and host range of stemrust.

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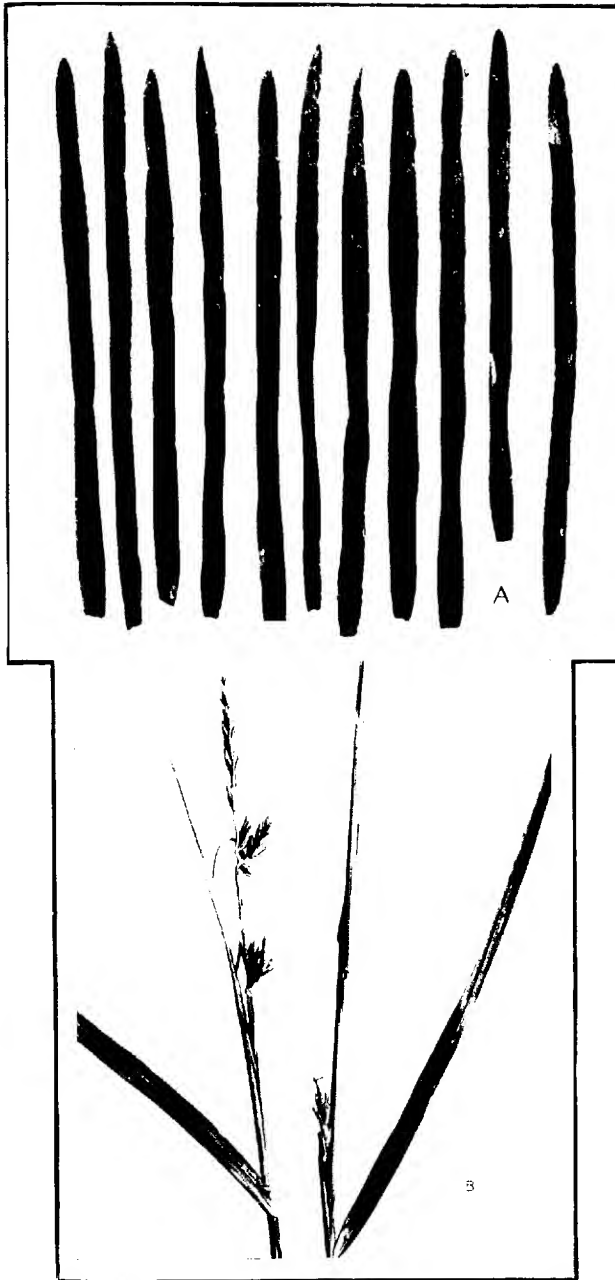
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PLATE 13

Puccinia graminis tritici

A.—On seedlings of Bobs wheat (CI 5047).

B.—On susceptible first-generation hybrid, Haynes Bluestem (Minnesota 169) ×
Kubanka durum wheat (CI 2094).



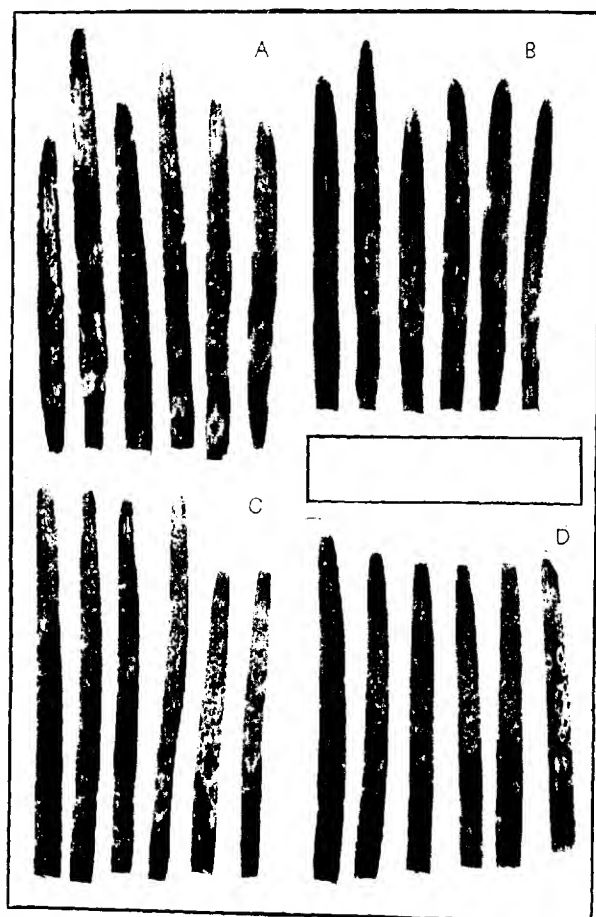


PLATE 14

Puccinia graminis tritici

A.—On seedlings of Haynes Bluestem inoculated with rust from the susceptible parent—that is, Haynes Bluestem.

B.—On seedlings of Haynes Bluestem, the susceptible parent, inoculated with rust from the susceptible first-generation hybrid 16(2×3)1.

C.—On seedlings of partially resistant durum parent, Kubanka (CI 2094), inoculated with rust from the susceptible parent, Haynes Bluestem (Minnesota 169).

D.—On seedlings of partially resistant durum parent, Kubanka (CI 2094), inoculated with rust from the susceptible first-generation hybrid 16(2×3)1.

PLATE 15.

Puccinia graminis tritici

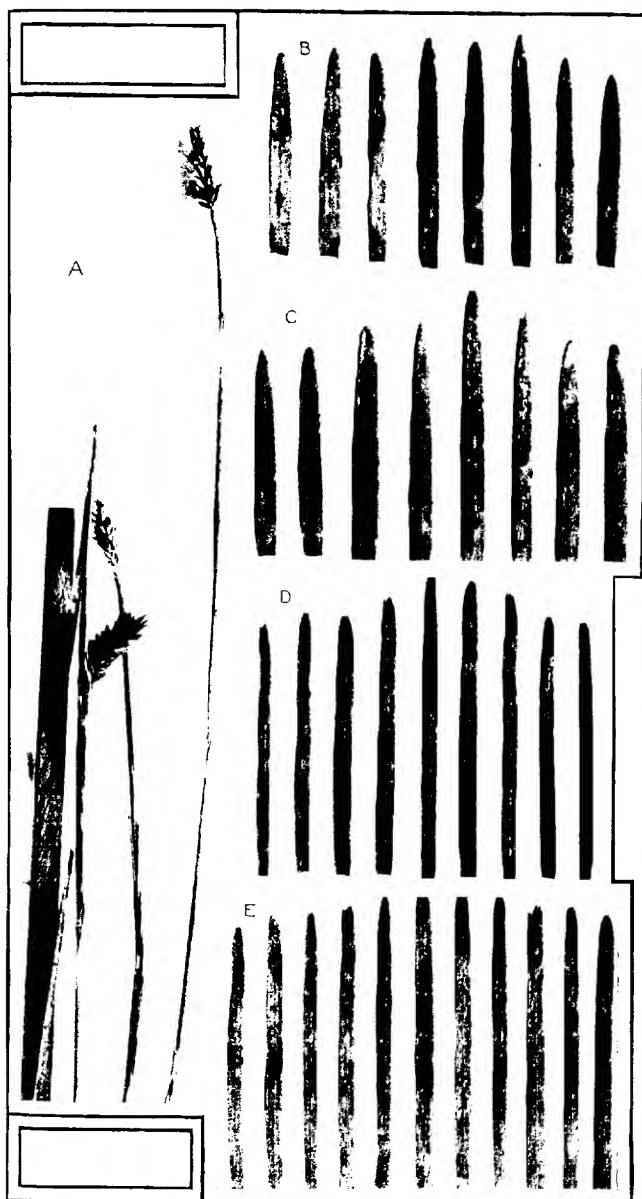
A.—Inoculations made on plants of susceptible second-generation hybrid of the cross emmer (Minnesota 1165) \times Marquis.

B.—Seedlings of the susceptible parent, Marquis, inoculated with rust from the susceptible second-generation hybrid 15(8 \times 1)1.

C.—Seedlings of the susceptible parent, Marquis, inoculated with rust from the stock cultures.

D.—Seedlings of extremely resistant parent, emmer (Minnesota 1165), inoculated with rust from the stock cultures.

E.—Seedlings of extremely resistant parent, emmer (Minnesota 1165), inoculated with rust from the susceptible second-generation hybrid 15(8 \times 1)1.



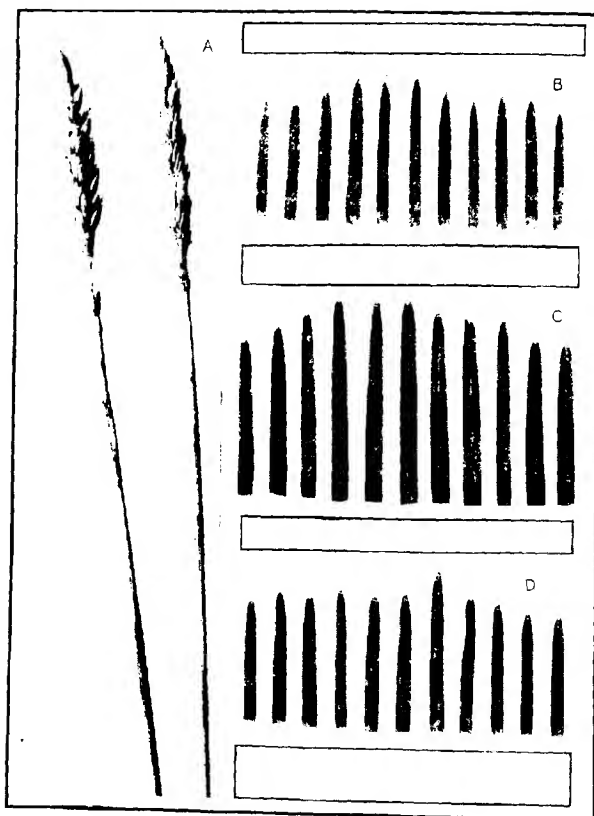


PLATE 16

Puccinia graminis tritici

A.—Susceptible second-generation plants from the cross Marquis \times Kubanka (CI 2094), inoculated with rust from the stock cultures.

B.—Seedlings of susceptible parent, Marquis, inoculated with rust from the susceptible second-generation plants shown in A.

C.—Seedlings of partially resistant parent, Kubanka (CI 2094), inoculated with rust from the stock cultures.

D.—Seedlings of partially resistant parent, Kubanka (CI 2094), inoculated with rust from susceptible second-generation plants shown in A.

PLATE 17

Puccinia graminis tritici

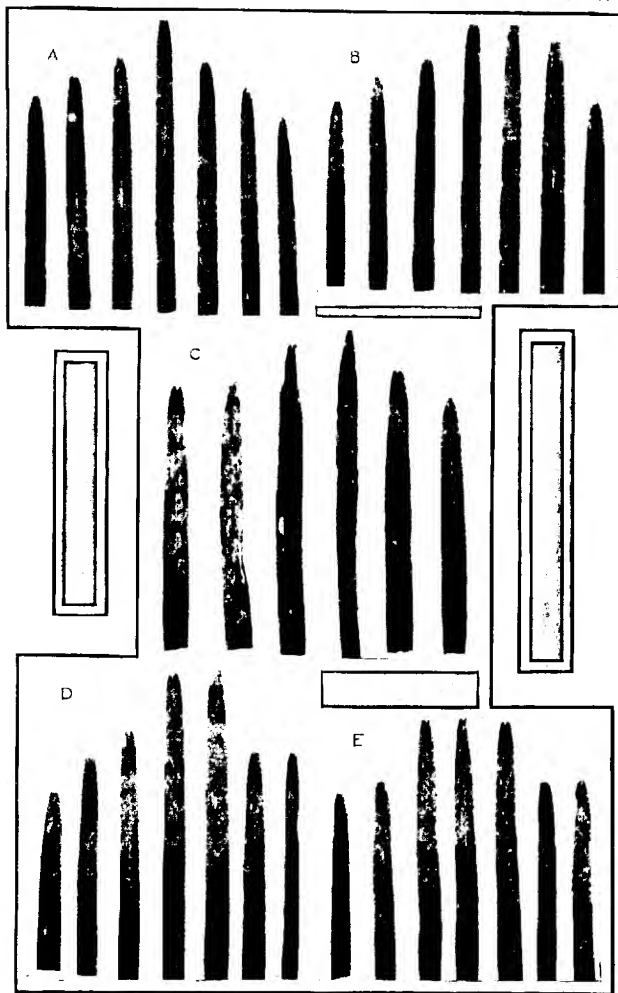
A.—Seedlings of susceptible parent, Haynes Bluestem (Minnesota 169), inoculated with rust from stock cultures.

B.—Seedlings of susceptible parent, Haynes Bluestem (Minnesota 169), inoculated with rust from the partially resistant F_9 hybrid $(4 \times 3)8AA$ shown in C.

C.—Seedlings of partially resistant F_9 hybrid $(4 \times 3)8 AA$ inoculated with rust from stock cultures.

D.—Seedlings of partially resistant parent, Kubanka (CI 2094), inoculated with rust from stock cultures.

E.—Seedlings of partially resistant parent, Kubanka (CI 2094), inoculated with rust from partially resistant F_9 hybrid $(4 \times 3)8AA$ shown in C.



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